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INVITED REVIEW

Evidence of current impact of climate change on life: a walk from genes to the biosphere

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Abstract

We review the evidence of how organisms and populations are currently responding to climate change through phenotypic plasticity, genotypic evolution, changes in distribution and, in some cases, local extinction. Organisms alter their gene expression and metabolism to increase the concentrations of several antistress compounds and to change their physiology, phenology, growth and reproduction in response to climate change. Rapid adaptation and microevolution occur at the population level. Together with these phenotypic and genotypic adaptations, the movement of organisms and the turnover of populations can lead to migration toward habitats with better conditions unless hindered by barriers. Both migration and local extinction of populations have occurred. However, many unknowns for all these processes remain. The roles of phenotypic plasticity and genotypic evolution and their possible trade-offs and links with population structure warrant further research. The application of *omic* techniques to ecological studies will greatly favor this research. It remains poorly understood how climate change will result in asymmetrical responses of species and how it will interact with other increasing global impacts, such as N eutrophication, changes in environmental N : P ratios and species invasion, among many others. The biogeochemical and biophysical feedbacks on climate of all these changes in vegetation are also poorly understood. We here review the evidence of responses to climate change and discuss the perspectives for increasing our knowledge of the interactions between climate change and life.

Keywords: biosphere, climate change, community, drivers of global change, drought, ecosystem, evolution, extinction, feedbacks, genomics, genotype, growth, metabolomics, migration, phenology, phenotype, population, warming

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Introduction. Rapid atmospheric and climate change

Elevated concentrations of atmospheric greenhouse gases have changed global climate, raising the Earth's surface temperature by 0.74 °C in the past century (IPCC, 2007). The main cause is the rise in concentration of atmospheric CO_2 from 280 ppm at the beginning of the industrial revolution to the current 394 ppm (Tans, 2012). This rapid rise has few precedents in Earth's history, at least in the last 500 million years (Mora *et al.*, 1996; Petit *et al.*, 1999; Beerling, 2002). The current rise continues to increase exponentially despite the few global policies aimed at stopping it; (Peñuelas & Carnicer, 2010; Carnicer & Peñuelas, 2012) for example, an increase in 2.36 ± 0.09 ppm of CO_2 in 2010 was one of the largest annual increases in recent decades (Peters *et al.*, 2012), suggesting that levels of CO_2 are likely to increase further and at faster rates. The current increase in concentrations of atmospheric CO_2 is equivalent to 71.8 ppm of CO_2 per century, which is several orders of magnitude greater than the rates of CO_2 increase observed in Earth's atmosphere in previous periods of rapid changes in atmospheric CO_2: 0.003–0.012 ppm during the Paleozoic (Mora *et al.*, 1996), 0.0075–0.012 ppm during the Cenozoic (Beerling, 2002) or 0.8–1 ppm during the last glaciation (Petit *et al.*, 1999). To the current rapid increase in atmospheric CO_2 concentrations, we must add the increases in the concentrations of other greenhouse gases such as methane and nitrogen oxides that are also increasingly emitted

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by human activities (IPCC 2007). This rapid increase in the atmospheric concentrations of CO_2 and other greenhouse gases has the potential to drive current climatic changes more quickly than all previous climatic changes (IPCC 2007). These rapid changes may exceed the capacities of individuals, populations and communities to assimilate them. Therefore, an immediate key question in the biology of global change is how the Earth-life system is coping with this new situation.

In this study, we review evidence of current biological impacts of climate change, the capacity of terrestrial organisms, populations, communities and ecosystems to cope with current climate change, and the upscaling of their responses, from the molecular and genetic level to the levels of community, ecosystem and biosphere (Fig. 1). We also identify some of the remaining questions warranting further research for better understanding the capacity of terrestrial organisms, populations, communities and ecosystems to adapt to climate change, including the interactions with other drivers of global change, and for better understanding the possible feedbacks on climate of these changes in organisms, populations, communities and ecosystems.

Responses of organisms

Molecular

Several studies have observed important phenotypic responses of organisms to drought and warming at the molecular level (Table 1). Ecometabolomic studies (Sardans *et al.*, 2011; Rivas-Ubach *et al.*, 2012) are a promising approach for gaining knowledge of the molecular plasticity of the responses of organisms to drought and warming. For example, relative to control individuals, *Erica multiflora* plants subjected to drought exhibited increased concentrations of antioxidant compounds, such as quinic and tartaric acid, and of elements such as K, and lower concentrations of sugars, amino acids and P (Rivas-Ubach *et al.*, 2012). These ecometabolomic studies allow the detection of the main metabolic pathways responsible for organismic responses and further help to recognize the genes involved in the response. The application of these emerging *omic* techniques to ecological and ecophysiological studies has already illustrated the large capacity of plants and animals to present plastic molecular responses to drought and warming. Molecular responses of plants to drought include increases in the concentrations of several enzymes as a result of the enhanced expression of some genes responsive to drought (Table 1), in particular the genes of the synthetic pathways of abscisic acid (ABA) and proline, and the mobilization of soluble sugar from stored polysaccharides (Table 1). These changes in gene expression are thereafter related to shifts in metabolomic structure (Alvarez *et al.*, 2008; Selter *et al.*, 2010; Krugman *et al.*, 2011; Sardans *et al.*, 2011; Rivas-Ubach *et al.*, 2012; Spieb *et al.*, 2012; Warren *et al.*, 2012) (Fig. 2). For example, the genes involved in drought tolerance are frequently related to the maintenance of turgor and cell integrity (Chang *et al.*, 1996; Rabello *et al.*, 2008; Foito *et al.*, 2009; Aranjuelo *et al.*, 2011; Erxleben *et al.*, 2012). Some compounds such as proline, phenolics, ABA, gamma aminobutyric acid (GABA) and soluble and alcohol sugars are frequently involved in the responses of plants to drought (Table 1). The mechanisms and molecules stimulated by drought protection, though, are very diverse among different species (Carmo-Silva *et al.*, 2009; Hamanishi & Campbell, 2011; Warren *et al.*, 2012) and even among different genotypes of the same species (Regier *et al.*, 2009; Cohen *et al.*, 2010; Hamanishi *et al.*, 2010; Yang *et al.*, 2010; Saxena *et al.*, 2011; Sanchez *et al.*, 2012; Warren *et al.*, 2012).

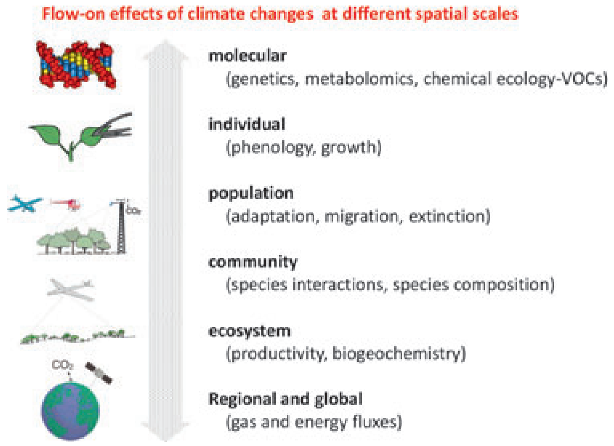

Fig. 1 Impacts from climate change on life at different spatial scales from the molecular to the biospheric levels.

Similarly, individual plants also change molecular composition in response to warming. *Omic* studies have revealed higher levels of expression of some genes (Zhang *et al.*, 2005a) and increased synthesis of some heat-stress proteins (Table 1) and of other metabolites and in other metabolic pathways (Guy *et al.*, 2008; Sardans *et al.*, 2011) (Table 1). Some studies suggest an increase in some pathways of protein catabolism linked to a rise in the synthesis of protective antistress proteins (Xu & Huang, 2008a,b, 2010; Xu *et al.*, 2008). Other studies show changing genotypic compositions at the population level in response to drought and/or warming (Jump *et al.*, 2006a, 2008).

The mechanisms of molecular responses to warming strongly differ when comparing different plant species, even those belonging to the same genus (Xu & Huang,

Table 1 *Omic* studies that have analyzed phenotypic responses to drought and warming at the molecular level

Species	Analytical techniques used	Principal results	References
Molecular responses of organisms to DROUGHT			
Capsicum annuum	Target metabolomics (HPLC-UV)	↑ Phenolics	Estiarte *et al.* (1994)
Zea mays	Metabolomics (HPLC-MS/MS)	↑ Threonine, GABA, 6-benzylaminopurine, proline, tryptophan, leucine	Alvarez *et al.* (2008)
Medicago sativa	Metabolomics (GC-MS)	↑ Proline, *p*-pinitol	Aranjuelo *et al.* (2011)
Eucalyptus sp.	Metabolomics (capillary GC)	↑ Carbohydrates, quercitol, polyols	Arndt *et al.* (2008)
Cynodon dactylon, *Zoysia japonica*	Metabolomics (GC-MS)	↑ 5-hydroxynorvaline	Carmo-Silva *et al.* (2009)
Pisum sativum	Metabolomics (^{1}H NMR)	↑ Proline, valine, threonine, homoserine, myoinositol, GABA	Charlton *et al.* (2008)
Vitis vinifera	Metabolomics (GC-MS)	↑ Glucose, maltose, proline	Cramer *et al.* (2007)
Physcomitrella patens	Metabolomics	↑ Proline, altrose, maltitol, ascorbic acid	Erxleben *et al.* (2012)
Lolium perenne	Metabolomics (GC-MS)	↑ Glucose, raffinose, fructose, trehalose, maltose ↓ Fatty acids	Foito *et al.* (2009)
Oryza sativa	Metabolomics (^{1}H NMR)	↑ Glucose, glutamate, glutamine	Fumagalli *et al.* (2009)
Stagonosphera nodorum	Metabolomics (GC-MS)	↑ Glycerol, arabitol ↓ Several amino acids	Lowe *et al.* (2008)
Arabidopsis sp.	Metabolomics (^{1}H NMR, HPLC-UV)	↑ Proline, tyrosine, malate, GABA	Lugan *et al.* (2009)
Solanum tuberosum	Metabolomics	↑ Sucrose, trehalose	Mane *et al.* (2008)
Belgica antartica	Metabolomics (GC-MS)	↑ Glycerol, erythritol, serine	Michaud *et al.* (2008)
Lupinus albus	Metabolomics (^{13}C NMR)	↑ Sucrose, glucose, proline	Peuke & Rennenberg (2004)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Sucrose, maltose, glucose, proline	Rizhsky *et al.* (2004)
Erica multiflora	Metabolomics (^{1}H NMR)	↑ Polyphenolics, quinic acid, choline, tartaric acid	Rivas-Ubach *et al.* (2012)
Lotus sp.	Metabolomics (GC-MS)	↑ Proline, sugars ↓ Aspartic acid, glutamic acid, serine, threonine	Sanchez *et al.* (2012)
Solanum sp.	Metabolomics (GC-MS)	↑ Alanine, GABA, β-alanine, homoserine, isoleucine, proline, serine, valine ↓ Glutamine, glycine, cysteine	Semel *et al.* (2007)
Eucalyptus sp.	Metabolomics (GC-MS)	↑ Sugars and sugar alcohols but in different intensities in different species	Warren *et al.* (2012)
Medicago sativa	Metabolomics(HPLC)	↑ Sucrose, succinate, malate	Naya *et al.* (2007)
Gossypium hirsutum	Metabolomics	↑ Several amino acids, proline, polyphenols	Parida *et al.* (2007)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Several amino acids and raffinose	Urano *et al.* (2009)
Oriza sativa	Proteomics	22 proteins associated with drought tolerance were identified	Rabello *et al.* (2008)
Quercus robur	Proteomics	18 proteins associated with drought tolerance were identified	Sergeant *et al.* (2011)
Glycine max	Proteomics	5 proteins increased and 21 decreased under drought	Alam *et al.* (2010)
Populus × *euramericana*	Proteomics	↑ Antioxidant proteins	Bonhomme *et al.* (2009)
Populus sp.	Proteomics	↑ Proteins associated with photosynthesis and some protein families related to cellular water transfer ↓ Some protein families related to cellular water transfer	Plomion *et al.* (2006)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Medicago sativa	Proteomics	↑ Rubisco protein	Aranjuelo *et al.* (2011)
Oryza sativa	Proteomics	↑ Superoxide dismutase	Muhammad Ali & Komatsu (2006)
Pinus armandii	Proteomics	5 proteins changed their concentrations under drought	He *et al.* (2007)
Populus sp.	Proteomics	↑ Rubisco protein ↓ Membrane-related proteins	Durand *et al.* (2011)
Quercus ilex	Proteomics	↑ Triosephosphate isomerases, rubisco activase ↓ Peroxidase	Echevarría-Zomeño *et al.* (2009)
Populus kangdingensis	Proteomics	↑ Proteins related to redox homeostasis and sugar metabolism	Yang *et al.* (2010)
Populus × euramericana	Proteomics	↓ Proteins related to photosynthesis	He *et al.* (2008)
Populus cathayana	Proteomics	↑ Proteins related to antithermal stress, secondary metabolism and defense	Xiao *et al.* (2009)
Triticum aesticum	Proteomics	↑ Some globulin, gliadin and albumin proteins	Yang *et al.* (2011)
Triticum aesticum	Proteomics	↑ Expression of 36 proteins	Caruso *et al.* (2009)
Populus cathayana	Proteomics	↓ Proteins related to photosynthesis	Zhang *et al.* (2010a)
Carissa spinarum	Proteomics	↓ Proteins related to photosynthesis	Zhang *et al.* (2010b)
Solanum tuberosum	Transcriptomics	↑ Raffinose and proline synthesis pathways ↓ Superoxide dismutase synthesis	Mane *et al.* (2008)
Lolium perenne	Transcriptomics	↑ Sulfate transporter protein	Foito *et al.* (2009)
Lotus sp.	Transcriptomics	↓ Proteins related to the synthesis of threonine, serine and glutamic acid	Sanchez *et al.* (2012)
Pinus radiata	Transcriptomics	Expression of 73 genes ♦ Expression of 43 genes	Heath *et al.* (2002)
Populus balsamifera	Transcriptomics	↑ Galactinol synthetase, stachyose synthetase	Hamanishi *et al.* (2010)
Pinus pinaster	Transcriptomics	↑ Glycolate oxidase synthesis	Dubos & Plomion (2003)
Pinus taeda	Transcriptomics	Variation in expression of 42 genes	Lorenz *et al.* (2005)
Pinus pinaster	Transcriptomics	↑ Expression of 28 genes ↓ Expression of 20 genes	Dubos *et al.* (2003)
Pinus taeda	Transcriptomics	↑ Expression of genes involved in cell-wall reinforcement	Chang *et al.* (1996)
Populus alba	Transcriptomics	↑ Expression of 199 genes (among them enzymes related to protein degradation) ↓ Expression of 253 genes (among them enzymes related to cellulose synthesis)	Berta *et al.* (2010)
Populus sp.	Transcriptomics	↑ Expression of genes linked to leaf abscission	Street *et al.* (2006)
Physcomitrella patents	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Cuming *et al.* (2007)
Lotus japonicus	Transcriptomics	↑ Expression of genes related to proline synthesis pathway	Díaz *et al.* (2010)
Lolium perenne	Transcriptomics	↑ Expression of genes related to glutathione peroxidase and superoxide dismutase synthesis pathways	Liu & Jiang (2010)
Hordeum vulgare	Transcriptomics	↑ Upregulation of the enzymes linked to ABA synthesis pathway	Seiler *et al.* (2011)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Arabidopsis thaliana	Transcriptomics	↑ Expression of genes related to control of stomatal openness	Aubert *et al.* (2010)
Populus sp.	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Cohen *et al.* (2010)
Nicotina tabacum	Transcriptomics	↑ Expression of genes related to proline and superoxide dismutase synthesis pathways	Li & Han (2012)
Festuca mairei	Transcriptomics	464 transcript fragments were differently expressed under drought ↓ Expression of genes related to transcription and DNA processing	Wang & Bughrara (2007)
Cleistogenes songorica	Transcriptomics	↑ Expression of 8 genes ↓ Expression of 5 genes	Zhang *et al.* (2011a)
Avena barbata	Transcriptomics	↓ Expression of genes related to N remobilization	Swarbreck *et al.* (2011)
Oriza sativa	Transcriptomics	↑ Expression of genes related to cell turgor	Rabello *et al.* (2008)
Populus balsamifera	Transcriptomics	↑ Expression of genes related to raffinose synthesis pathway	Hamanishi *et al.* (2010)
Populus nigra	Transcriptomics	↑ Expression of genes related to starch mobilization to produce soluble sugars	Regier *et al.* (2009)
Zea mays	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Jiang *et al.* (2012)
Gossypium sp.	Transcriptomics	↑ Expression of genes related to cell-wall loosening and cell expansion	Padmalatha *et al.* (2012)
Quercus suber	Transcriptomics	↑ Expression of genes related to glucose, fructose, galactose, manitol and quercitol synthesis pathways	Spieb *et al.* (2012)
Populus nigra	Transcriptomics	↑ Expression of genes related to starch degradation pathways	Regier *et al.* (2009)
Avena barbata	Transcriptomics	↓ Expression of genes related to C and N metabolism	Swarbreck *et al.* (2011)
Medicago sativa	Transcriptomics	↑ Sucrose synthetase and nitrogenase	Naya *et al.* (2007)
Oryza sativa	Transcriptomics	↑ Synthesis of transcriptomic factor protein AP37	Oh *et al.* (2009)
Arabidopsis sp.	Transcriptomics	↑ Synthesis of protein LEW1 linked to dolichol biosynthesis pathway	Zhang *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ DREB2A expression	Perera *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Drought-inducible genes and discovery of DRIP1 and DRIP2 genes involved in DREBA protein proteolysis	Qin *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Discovery of OCP3 transcription factors that actuate a drought ABA-responsive mechanism	Ramírez *et al.* (2009)
Solanum tuberosum ssp. *andigena*	Transcriptomics	↑ Sucrose phosphatase and glucose pyrophosphatase transcription	Watkinson *et al.* (2008)
Triticum durum, *Aegilops kotschii*, *Aegilops umbellulata*	Transcriptomics	↑ Expression of 5 dehydrin genes	Rabello *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ DREB2A expression that stimulates the expression of drought-responsive genes	Sakuma *et al.* (2006)
Arabidopsis sp.	Transcriptomics	↑ Discovery of the gene encoding protein nucleotidase/phosphatase SAL1 that is a negative regulator of drought-tolerance genes	Wilson *et al.* (2009)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Arabidopsis sp.	Transcriptomics	↑ Discovery of the gene encoding the factor HYB96 that is upregulated under drought and integrates ABA and auxin signals under drought	Seo *et al.* (2009)
Nicotina tabacum	Transcriptomics	↑ Receptor kinase protein was related and cytokinin-dependent photorespiration protein that increases plant resistance to drought	Rivero *et al.* (2009)
Thellungiella halophila	Transcriptomics	↑ Synthesis of vacuolar pyrophosphatase	Li *et al.* (2008a,b)
Zea mays	Transcriptomics	↑ 51 transcripts	Fernandes *et al.* (2008)
Cajanus cajan	Transcriptomics	↑ Expression of hybrid proline-rich protein	Priyanka *et al.* (2010)
Arabidopsis thaliana	Transcriptomics	Discovery of the gene related to the feedback mechanisms between responses to drought and changes in the circadian clock	Legnaioli *et al.* (2009)
Tabacum sp.	Transcriptomics	↑ Expression of phospholipases that increased drought resistance at short-term	Hong *et al.* (2008)
Arabidopsis sp., *Brassica napus*	Transcriptomics	↓ Expression of farnesyltransferase	Wang *et al.* (2009)
Oryza sativa	Transcriptomics	Discovery of the gene encoding mitogen-activated protein kinase that mediates in drought tolerance by scavenging reactive oxygen species	Ning *et al.* (2010)
Arabidopsis sp.	Transcriptomics	↑ Expression of two genes (PUB22 and PUB 23)	Cho *et al.* (2008)
Molecular responses of organisms to WARMING			
Saussurea alpina, *Tofieldia pusilla*, *Carex vaginata*, *Vaccinium ulginosum*, *Salaginella selaginoides*	HPLC-UV (target metabolomics)	No effects on plant secondary compounds	Nybakken *et al.* (2011)
Arabidopsis thaliana	Metabolomics (GC-MS)	↑ Several sugars, leucine, valine, tyrosine, uracil, quinic acid, xylitol	Kaplan *et al.* (2004)
Agrostis stolonifera	Metabolomics (GC-MS)	↑ Lipid unsaturation	Larkindale & Huang (2004)
Drosophila sp.	Metabolomics (^{1}H NMR)	↑ Leucine, valine, tyrosine	Malmendal *et al.*, 2006;
Belgica antarctica	Metabolomics (GC-MS)	↓ Serine	Michaud *et al.* (2008)
Schizosaccharomyces pombe	Metabolomics (LS-MS)	↑ Some amino acids, threhalose, glycerophosphoethanolamine, arabitol, ribulose, ophthalmic acid Many changes in secondary metabolites such as ↓ urea-cycle intermediates and ↑ acetylated compounds	Pluskal *et al.* (2010)
Erica multiflora	Metabolomics (^{1}H NMR)	↑ Fatty acids, compounds related to amino acid and sugar metabolism	Rivas-Ubach *et al.* (2012)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Sucrose, maltose, glucose	Rizhsky *et al.* (2004)
Oncorhynchus mykiss	Metabolomics (^{1}H NMR)	Different metabolomic fingerprinting	Turner *et al.* (2007)
Oncorhynchus mykiss	Metabolomics (^{1}H NMR)	↑ Metabolites related to antithermal stress protein pathways, ATP, glycogen	Viant *et al.* (2003)
Folsomia candida	Metabolomics (^{1}H NMR)	↓ Arginine, lysine, leucine, phenylalanine, tyrosine (after 7 hr heat exposure)	Waagner *et al.* (2010)
Oryza sativa	Metabolomics (Capillary electrophoresis-MS)	↑ Sucrose, pyruvate/oxaloacetate-derived amino acids ↓ Sugar phosphates and organic acids involved	Yamakawa & Hakata (2010)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
		in glycolysis/gluconeogenesis and the tricarboxylic acid cycle (TCA)	
Macrosiphum euphorbiae	Proteomics	↓ Proteins involved in energy metabolism	Nguyen *et al.* (2009)
Agrostis scabra, *Agrostis stolonifera*	Proteomics	↑ Proteins involved in photosynthesis and heat-shock proteins	Xu & Huang (2008a,b, 2010) and Xu *et al.* (2008)
Pinus armandii	Proteomics	8 proteins changed their concentrations under warming	He *et al.* (2007)
Triticum aesticum	Proteomics	↑ Some gluteninss proteins	Yang *et al.* (2011)
Festuca sp.	Transcriptomics	↑ Expression of genes related to transcription and photosynthesis	Zhang *et al.* (2005a)
Avena barbata	Transcriptomics	↑ Expression of genes related to N remobilization	Swarbreck *et al.* (2011)
Arabidopsis sp.	Transcriptomics	↑ Protein BOBBER1	Perez *et al.* (2009)
Arabidopsis sp.	Transcriptomics	↑ Expression of NFYAS5 transcription factor that is related to the transcription of stress-response genes	Li *et al.* (2008a,b)
Solanum tuberosum	Transcriptomics	↑ Genes related to cell proliferation, hormone synthesis and antistress mechanisms were upregulated	Ginzberg *et al.* (2009)
Boea hygrometrica	Transcriptomics	↑ Expression of BhHsf1 transcriptional factor that is related to thermotolerance	Zhu *et al.* (2009)
Zea mays	Transcriptomics	↑ 754 transcripts	Fernandes *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Expression of peptidyl prolyl cis/trans isomerase	Meiri & Breiman (2009)
Arabidopsis sp.	Transcriptomics	Epression of dehydration-response element binding protein (DREB2A)	Schramm *et al.* (2008)
Oryza sativa	Transcriptomics	↑ Expression of 23 genes related to heat-shock protein synthesis	Sarkar *et al.* (2009)
Chenopodium album	Transcriptomics	↑ Expression of heat-shock proteins	Barua *et al.* (2008)

2008b, 2010; Xu *et al.*, 2008). The experimental data currently available suggest that the response of plants to warming does not imply important changes in secondary compounds. For example, Nybakken *et al.* (2011) observed that warming had little effect on the concentrations of carbon-based secondary compounds in subalpine ecosystems.

The individual molecular responses of plants to drought and warming are frequently related to physiological (Xu & Zhou, 2006; He *et al.*, 2008; Aubert *et al.*, 2010; Yang *et al.*, 2010; Aranjuelo *et al.*, 2011), phenological (Swarbreck *et al.*, 2011) and anatomical (Spieb *et al.*, 2012) responses. Moreover, changes in the molecular composition of plants in response to drought are linked to changes in elemental stoichiometry (Rivas-Ubach *et al.*, 2012) (Fig. 2), with different levels of response among the species of the same community (Peñuelas *et al.*, 2008a). Changes in plant C : N : P stoichiometry affect the cycling of nutrients in ecosystems, the transfer of energy throughout trophic webs and the composition of herbivore communities (Elser *et al.*, 2000, 2009; Elser, 2006; Sardans *et al.*, 2012a). All these shifts in the chemical composition of plants can thus have further consequences on the functioning of trophic webs (Peñuelas & Sardans, 2009), which warrants future research based mainly on long-term observations and experiments.

Studies on the molecular impacts of drought and warming on wild terrestrial animals are less common. Nguyen *et al.* (2009) observed that individual aphids exposed to elevated temperatures presented lower growth, lower abundances of several enzymes of central pathways of energy metabolism and increased production of exoskeletal proteins. Metabolomic studies in insects further confirmed that heat stress increases the levels of some amino acids and proteins and decreases the metabolism of sugar (Malmendal *et al.*, 2006; Michaud *et al.*, 2008) (Table 1).

This overview of current bibliography of omic studies of the impacts of climate change shows that these techniques have a high sensitivity to detect metabolome shifts of organisms submitted to drought and/or warming. They show a fast increase in the synthesis of enzymes, metabolic pathways and metabolites linked

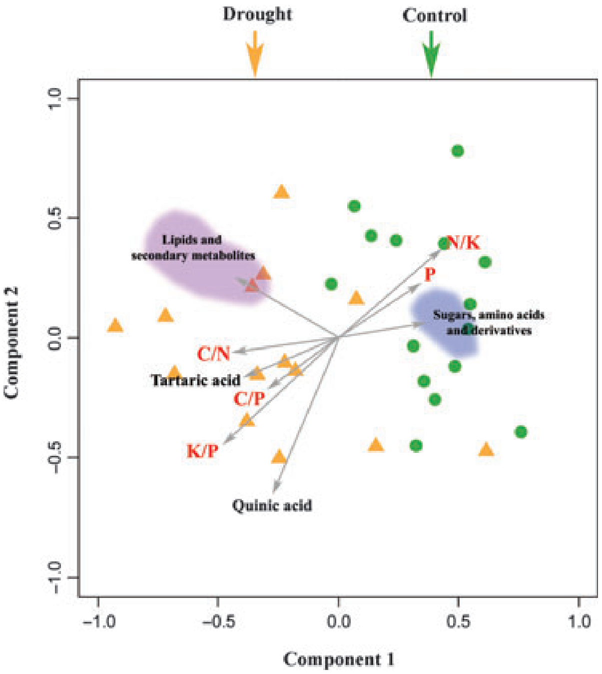

Fig. 2 PLS-DA analysis of the stoichiometry and metabolomics of leaves of *Erica multiflora* shrubs submitted to the effects of a moderate experimental field drought (Based on Rivas-Ubach *et al.*, 2012). (triangles: drought; circles: control).

to osmotic control and antistress mechanisms. However, there is a lack of studies coupling climatic change and genomics-metabolomics with nutrient cycles, availability and stoichiometry, with physiological and phenological changes and with shifts in ecosystem structure. These integrated studies should provide a better understanding of the mechanisms and processes underlying the change in resource use, in intraspecies and interspecies competition and in species substitution and selection under global change.

Physiological and morphological

An organism's capacity for physiological adaptation is a key factor in its success in adapting to climate change (Bernardo *et al.*, 2007). A plant's response to drought includes several physiological responses. There are changes in the allocation of resources, decreases in net photosynthetic rate, decreases in efficiency of carboxylation, increases in the efficiency of PSII photochemistry and increases in water use efficiency (WUE) that frequently accompany a decrease in plant growth and reproductive output, the intensities of which differ among communities and species (Table 2). The shifts in enzymatic machinery necessary for these changes are linked to shifts in N metabolism, consisting of a decrease in the activity of key enzymes related to N anabolism, such as nitrate reductase and glutamine synthase, and an increase in enzymatic activity related to N catabolism and transport, such as the activity of asparaginase (Xu & Zhou, 2006). As reported in the previous section, a shift of protein content occurs under drought from proteins related to photosynthesis and carboxylation to proteins linked to antistress systems (Table 1). Fine-scale studies using ^{1}H nuclear magnetic resonance (NMR) imaging have observed that leaves of the Mediterranean tree *Quercus ilex* under prolonged drought are able to maintain water in parenchymal tissues for a longer time than in vascular tissues, which allows the most active parts of the leaves to be more hydrated for a longer time (Sardans *et al.*, 2010). These conservative mechanisms are frequently able to minimize the negative effects of drought on plant growth (Molina-Montenegro *et al.*, 2011; Peñuelas *et al.*, 2011a, b). These mechanisms also have negative impacts, however, such as a decrease in nutrient uptake resulting from the decrease in plant transpiration (Peñuelas *et al.*, 1993; Cramer & Hawkins Verboom, 2009; Cernusak *et al.*, 2011) or a decrease in the production of root phosphatases (Sardans *et al.*, 2007). Plants can compensate for this low uptake of nutrients by enhancing their reabsorption of nutrients (Heckathorn & DeLucia, 1994; Devakumar *et al.*, 1999; Marchin *et al.*, 2010). This increased reabsorption, together with a higher synthesis of C-rich secondary compounds under drought (Hale *et al.*, 2005), decrease the quality of leaf litter, which has a negative feedback effect on productivity by decreasing, decomposition rates of soil organic matter and the availability of nutrients (Yaire & van Cleve, 1996; Sardans & Peñuelas, 2004, 2005).

An organism's response to warming depends on whether or not the ecosystem is limited by water and on whether or not the climate is cold (Table 2). In ecosystems not limited by water, the photosynthetic capacity of plants and, in general, the changes in plant function under warming strongly depends on the capacity of each species to adapt its optimal temperature of maximal rates of assimilation (Gunderson *et al.*, 2010; Sardans & Peñuelas, 2010; Zelikova *et al.*, 2012). Plants generally tend to increase their optimal photosynthetic temperatures under warming, which differ among species (Gunderson *et al.*, 2010). This photosynthetic acclimation can increase plant production capacity if other resources such as nutrients are not limiting. In this way, the capacity of a plant to invest in mechanisms for enhancing the availability and uptake of nutrients is critical for enhancing growth (Michelsen *et al.*, 1996; Henry & Molau, 1997; Jónsdóttir *et al.*, 2005b). Plants under warming can respond by increasing N_2 fixation (Sorensen & Michelsen, 2011), mycorrhizal intensity (Rillig *et al.*, 2002; Staddon *et al.*, 2004; Olsrud *et al.*, 2010; Yergeau *et al.*, 2012), root enzymes

Table 2 Main results of available studies on the effects of drought and warming on growth, production (photosynthesis), reproductive capacity or resources use and allocation

Biome and species	Study type	Main results	Reference
Effects of drought			
Tropical forest (Gen *Shorea*, Gen *Dacrydium*, Gen *Payena*)	Field observation	↓ Growth in some species and no effects on growth in other species	Aiba & Kitayama (2002)
Temperate shrubland (*Calluna vulgaris*)	Field climate manipulation	↓ Photosynthetic activity	Albert *et al.* (2011a)
Temperate grassland (*Deschampsia flexuosa*)	Field climate manipulation	↓ Growth	Albert *et al.* (2011b)
Temperate grassland (*Alopecurus pratensis*, *Arrhenaterum elatius*, *Festuca pratensis*, *Holcus lanatus*)	Common garden	↓ Growth, but with different intensities depending on species	Belerkuhnlein *et al.* (2011)
Boreal forest (*Picea* sp.)	Common garden	↓ Photosynthetic activity	Bigras (2005)
Temperate grassland (*Festuca arundinacea*, *Poa pratensis*, *Festuca rubra*, *Agrostis capillaries*, *Stellaria graminea*, *Veronica chamaedrys*, *Vicia sativa*)	Field climate manipulation	↓ Growth	Bloor *et al.* (2010)
Mediterranean forest (*Pinus halepensis*)	Field climate manipulation	↓ Growth	Borghetti *et al.* (1998)
13 conifer species	Greenhouse	↑ WUE	Brodribb & Hill (1998)
Temperate forest (*Pinus ponderosa*)	Field gradient study	↓ Allocation of C to leaves	Callaway *et al.* (1994)
Temperate grassland (*Lotus corniculatus*)	Greenhouse	↑ Aboveground growth and reproductive output ↓ Belowground growth	Carter *et al.* (1997)
Semiarid grassland (*Cryptantha flava*)	Field climate manipulation	↓ Growth	Casper *et al.* (2006)
Mediterranean grassland (*Setaria parviflora*)	Field climate manipulation	↓ Growth	Chuine *et al.* (2012)
Mediterranean forest (*Quercus ilex*)	Field observation	↓ Growth	Corcuera *et al.* (2004)
Temperate forest (*Pinus ponderosa*)	Field observation	↓ Growth	Fernandez *et al.* (2012)
Vitis vinifera	Field climate manipulation	↓ Photosynthetic activity	Flexas *et al.* (2004)
Temperate grassland (*Hypericum perforatum*)	Field climate manipulation	↓ Growth and reproductive output	Fox *et al.* (1999)
Temperate and alpine grasslands	Field observation	↓ Belowground growth and inconclusive results on aboveground growth	Frank (2007)
Temperate shrubland (*Calluna vulgaris*, *Pteridium aquilinum*)	Common garden	↓ Growth	Gordon *et al.* (1999a,b)
Temperate forest (*Populus nigra*)	Greenhouse	↓ Growth and photosynthetic activity	Hale *et al.* (2005)
Temperate forest (*Acer rubrum*, *Acer saccharum*, *Betul papyrifera*, *Betula alleghamiensi*)	Field observation	↓ Growth, but with different intensities depending on the species	He *et al.* (2005)
Temperate grassland (*Dactylis glomarata*, *Elymus repens*, *Phleum pratense*, *Poa* sp., *Setaria glauca*, *Setaria viridis*, *Plantago lanceolata*, *Taraxacum officinalis*, *Potentilla argentea*, *Silene latifolia*, *Achillea millefolium*, *Tanacetum vulgare*)	Field climate manipulation	↓ Reproductive output	Hoeppner & Dukes (2012)
Pinus halepensis	Pot experiment	↓ Growth	Inclan *et al.* (2005)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Boreal forest (*Picea abies*)	Field climate manipulation	↓ Growth	Jyske *et al.* (2010)
Alpine forest (*Abies alba*)	Field observation	↓ Growth	Liancourt *et al.* (2012)
Mediterranean shrubland (*Erica multiflora, Globularia alypum*)	Field climate manipulation	↓ Photosynthetic activity	Llorens *et al.* (2003)
Mediterranean shrubland (*Erica multiflora, Globularia alypum*)	Field climate manipulation	↓ Growth	Alla *et al.* (2012), Lloret *et al.* (2004a,b), Loe *et al.* (2005)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↑ WUE	Lloret *et al.* (2004a,b)
Temperate forest (*Fagus sylvatica*)	Field observation	↓ Belowground growth	Meier & Leuschner (2008)
Mediterranean forest (*Pinus halepensis*)	Field observation	↓ Growth	Moreno-Gutiérrez *et al.* (2012)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↑ WUE	Ogaya & Peñuelas (2003)
Mediterranean forest (*Arbutus unedo, Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↓ Growth of *A. unedo* and *Q. ilex* No effects on *P. latifolia*	Ogaya & Peñuelas (2007a,b)
Rainforest	Review of field observational studies	↓ Growth and photosynthetic activity	Parolin *et al.* (2010)
Mediterranean forest (*Quercus ilex*)	Field climate manipulation	Changes in N allocation to leaves depending on drought intensity	Peña-Rojas *et al.* (2006)
Temperate and Mediterranean shrublands	Field climate manipulation	↓ Growth of Mediterranean shrublands and no effects on growth of temperate shrublands	Peñuelas *et al.* (2004a)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field observation	↑ WUE	Peñuelas *et al.* (2000a)
Mediterranean, semiarid and tropical biomes	Metadata analysis	↑ WUE	Peñuelas *et al.* (2011a,b)
Mediterranean forest (*Quercus ilex*)	Field climate manipulation	↓ Reproductive output	Pérez-Ramos *et al.* (2010)
Temperate forest (*Fagus sylvatica,*)	Pot experiment	↓ P allocation to leaves	Peuke & Rennenberg (2004)
Temperate forest (*Fagus sylvatica, Picea abies*)	Field observation	↓ Growth	Pretzsch & Dieler (2011)
Temperate shrublands (*Erica multiflora, Globularia, Pinus halepensis*)	Field climate manipulation	Different effects on photosynthetic activity depending on species and season	Prieto *et al.* (2009a)
Temperate shrublands (*Erica multiflora, Globularia, Pinus halepensis*)	Field climate manipulation	↓ Growth	Prieto *et al.* (2009b)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Temperate grassland (*Brassica napus*)	Common garden	↓ Growth	Qaderi *et al.* (2006)
Temperate forest	Review of field observational and experimental studies	↓ Photosynthetic activity	Rennenberg *et al.* (2006)
Temperate grassland (*Leymus chinensis*)	Field observation	↓ Growth and reproductive output	Renzhong & Qiong (2003)
Semiarid shrubland (*Larrea tridentate, Propopsis glandulosa*)	Field climate manipulation	No conclusive results regarding growth	Reynolds *et al.* (1999)
(*Alloteropsis semialata, Panicum aequinerve, Tristacya leucothrix, Themeda triandra*)	Pot experiment	↓ Photosynthetic activity	Ripley *et al.* (2010)
Mediterranean shrubland (*Globularia alypum, Erica multiflora, Dorycnium pentaphyllum*)	Field climate manipulation	↓ Allocation to leaves	Sardans *et al.* (2008a)
Continental shrubland (*Oryzopsis hymenoides, Gutierrezia sarothrae, Ceratoides lantana*)	Field climate manipulation	↓ Growth	Schwinning *et al.* (2005)
Mediterranean forest (*Quercus ilex, Phillyrea latifolia*)	Field climate manipulation	↓ Photosynthetic activity	Serrano & Peñuelas (2005)
Temperate grassland (*Phleum pratense, Trifolium repens, Rumex obtusifolium*)	Field climate manipulation	↓ Photosynthetic efficiency	Signarbieux & Feller (2011)
Temperate forest (*Pinus nigra*)	Common garden	No effects on growth	Thiel *et al.* (2012)
Temperate forest (*Quercus stellata, Junniperus virginiana, Schizachyrium scoparium*)	Field climate manipulation	↓ Photosynthetic activity	Volder *et al.* (2010)
Alpine forest (*Picea crassifolia*)	Field observation	↓ Growth	Wang *et al.* (2012)
Temperate forest (*Pinus taeda*)	Field climate manipulation	↓ Growth and photosynthetic activity	Wertin *et al.* (2012)
Mediterranean shrubland (*Leucadedron* sp., *Erica* sp., *Diastella divaricata*)	Field climate manipulation	↓ Growth of anisohydric species, isohydric species were unaffected	West *et al.* (2012)
Tropical grassland (*Pennisetum setaceum, Heteropogon contortus*)	Greenhouse	↓ Growth	Williams & Black (1994)
All biome types	Meta-analysis of 85 sites with field climate manipulation	↓ Growth	Wu *et al.* (2011a,b)
Temperate grassland (*Leymus chinensis*)	Field climate manipulation	↓ Photosynthetic activity	Xu & Zhou (2006)
Effects of warming			
Temperate shrubland (*Calluna vulgaris*)	Field climate manipulation	↑ Photosynthetic activity	Albert *et al.* (2011a)
Temperate grassland (*Deschampsia flexuosa*)	Field climate manipulation	↑ Growth	Albert *et al.* (2011b)
Tundra (13 different sites)	Field climate manipulation	↑ Growth in lower tundra and ↑ Growth in low tundra and	Arft *et al.* (1999)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
		↑ Reproductive output in high tundra sites	
Tundra (*Vaccinium sp.*, *Betula nana*, *Carex eusifolia*, lichen species)	Field climate manipulation	↑ Increase in growth of most species	Biasi *et al.* (2008)
Boreal forest (*Picea mariana*)	Field climate manipulation	↑ Growth	Bronson *et al.* (2009)
Tundra	Field climate manipulation	↑ Growth in shrub species ↓ Growth of nonvascular plants	Chapin *et al.* (1995)
Tundra (*Ceratodon purpureus*, *Bryum pseudotriquetrum*, *Bryoerythrophyllum recurvirostre*)	Field observation	↑ Growth, effect related to an increase in water availability	Clarke & Zani (2012)
Alpine shrubland (*Vaccinium myrtilus*, *Vaccinium gautheroides*, *Empetrum hermaphroditum*)	Field climate manipulation	↑ Growth of *V. myrtilus* and no effects on *V. gautheroides* and *E. hermaphroditum*	Dawes *et al.* (2011)
Tundra (*Deschampsia Antarctica*, *Colobanthus quitensis*)	Field climate manipulation	↑ Reproductive output	Day *et al.* (1999)
Temperate grassland (*Dactylis glomerata*, *Festuca arundinacea*, *Lolium perenne*, *Trifoliun repens*, *Medicago sativa*, *Plantago lanceolata*, *Bellis perennis*, *Rumex acetosa*)	Common garden	↓ Growth related to higher evapotranspiration and lower soil moisture	De Boeck *et al.* (2007, 2008)
Grassland of temperate forest understory (*Anemone nemorosa*, *Milium effusum*)	Field climate manipulation	↑ Growth and reproductive output	De Frenne *et al.* (2011)
Boreal peatland (*Sphagnum fuscum*)	Field climate manipulation	↑ Growth	Dorrepaal *et al.* (2003)
Alpine grassland	Field climate manipulation	↑ Belowground growth	Egli *et al.* (2004)
Tundra (46 different sites)	Field observation	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Elmendorf *et al.* (2012a)
Tundra (61 different sites)	Field climate manipulation	↑ Growth of shrubs in warmer sites and of herbs in colder sites	Elmendorf *et al.* (2012b)
Alpine grassland (*Poa alpina*, *Artemisia ginepi*, *Trifolium pallescens*, *Anthyllis vulneraria*)	Field climate manipulation	↑ Growth	Endels *et al.* (2007)
Tropical forest (*Cedrela odorata*, *Cliricidia sepium*)	Greenhouse	↑ Growth	Esmail & Oelbermann (2011)
Temperate forest	Field climate manipulation	↑ Growth of trees and shrubs but not herbs	Farnsworth *et al.* (1995)
Temperate grassland (*Andropogon gerardii*, *Sorghastrum mutans*, *Panicum*	Field climate manipulation	↓ Productivity in summer	Fay *et al.* (2011)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
virgatum, *Sporobolus asper*, *Solidago canadensis*, *Aster ericoides*, *Solidago missouriensis*)			
Temperate grassland (*Leymus chinensis*)	Field observation	↑ Reproductive output	Gao *et al*. (2012)
Temperate shrubland (*Calluna vulgaris*, *Pteridium aquilinum*)	Common garden	↑ Growth of *C. vulgaris*, and no effects on the growth of *P. aquilinum*	Gordon *et al*. (1999a,b)
Temperate grassland (*Juncus gerardii*, *Spartina patens*, *Spartina alterniflora*, *Plantago maritima*, *Analgis maritima*, *Atriplex patula*, *Glaux maritima*, *Suaeda maritima*)	Field climate manipulation	↑ Growth of *Plantago maritima* and ↓ growth of *Juncus gerardii*, *Spartina patens*	Gedan & Bertness (2009)
Temperate forest (*Liquidambar atyraciflua*, *Quercus rubra*, *Quercus falcate*, *Betula alleghaniensis*, *Populus grandidentata*)	Field climate manipulation	↑ Increases in the optimal temperature for maximal photosynthetic activity	Green (2010)
Subarctic shrubland (*Empetrum hemaphroditum*, *Vaccinum myrtilus*, *Vaccinum ulginosum*, *Vaccinum vitis-idaea*)	Field climate manipulation	↑ Growth	Hartley *et al*. (1999)
Subtropical grassland (*Eupatorium adenophorum*, *Eupatorium chinense*)	Pot experiment	↑ Growth, but more in the invasive species, *E. adenophorum*	He *et al*. (2012)
Tundra	Review of 26 field climate-manipulation experiments	↑ Growth depending on nutrient availability	Henry & Molau (1997)
Tundra (*Carex* sp.)	Field observational	↑ Growth	Hill & Henry (2011)
Tundra (several vascular and nonvascular plants)	Field climate manipulation	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Hobbie *et al*. (1999)
Temperate grassland (*Dactylis glomerata*, *Elymus repens*, *Phleum pratense*, *Poa sp.*, *Setaria glauca*, *Setaria viridis*, *Plantago lanceolata*, *Taraxacum officinale*, *Achillea millefolium*, *Potentilla argentea*, *Silene latifolia*, *Tanacetum vulgare*)	Field climate manipulation	No conclusive results regarding growth	Hoeppner & Dukes (2012)
Tundra (*Betula* sp.)	Field climate manipulation	No conclusive results regarding growth	Hofgaard *et al*. (2010)
Tundra (*Carex aquatilis*, *Salix rotundifolia* and several herb species)	Field climate manipulation	↑ Growth of herbs but not of the entire community	Hollister & Flaherty (2010)
Tundra	Field climate manipulation in 4 sites	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Hollister *et al*. (2005)
Tundra	Field climate manipulation	↑ Growth of grasses but not of the entire community	Hollister & Flaherty (2010)
Temperate grassland (Several C3 and C4 grasses)	Field climate manipulation		Hovenden *et al*. (2007)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
		↑ Reproductive output in perennial grasses but no effects in the other grass groups	
Temperate grassland (*Poa pratensis*, *Bromus mermis*, *Cirsium arvense*, *Lotus corniculatus*)	Field climate manipulation	↑ Growth	Hutchison & Henry (2010)
Alpine grassland (*Asterolasia trymalioides*, *Carex sp.*, *Celmsia pugioniformis*, *Plantago euryphylla*, *Poa hiemata*, *Pimela alpine*)	Field climate manipulation	↑ Growth	Jarrad *et al.* (2009)
Tundra (*Carex bigelowii*)	Field climate manipulation	↑ Growth	Jónsdóttir *et al.* (2005a)
Tundra (Diverse vascular and nonvascular plants)	Field climate manipulation	↑ Growth of vascular plants and ↓ growth of nonvascular plants but greater effects in nutrient-rich sites	Jónsdóttir *et al.* (2005b)
Temperate shrubland (*Calluna vulgaris*, *Deschampsia flexuosa*)	Field climate manipulation	No effects on growth	Kongstad *et al.* (2012)
Temperate grassland and shrublands	Common garden experiment	↑ Growth in grasses and ↓ growth in shrubs	Kreyling *et al.* (2011)
Temperate shrublands (*Ledum palustre*, *Empetrum nigrum*, *Vaccinium uliginosum*, *Arctous alpinus*, *Vaccinium vitis vinifera*)	Field climate manipulation	↑ Growth of evergreen shrubs and no effects on deciduous shrubs	Kudo & Suzuki (2003)
Alpine grassland (*Delphinium nuttallianum*, *Helianthella quinquenervia*, *Erythronium grandiflorum*, *Erigeron speciosus*)	Field climate manipulation	↑ Reproductive output of *D. nuttallianum* and *H. quinquinervia* and no effects in the other two species	Lambrecht *et al.* (2006)
Alpine grassland (diverse *Korbresia specis*, *Carex scabriopsis*, *Carex atrofusca*)	Field climate manipulation	↑ Growth	Li *et al.* (2011a)
Alpine grassland (*Potentilla anserina*, *Elymus nutants*, *Kobresias* species, *Anemone trullifolia*)	Field climate manipulation	↓ Growth due to ↑ of herbivorous activity	Li *et al.* (2011b)
Continental grassland (*Carex pediformis*, *Festuca lenensis*, *Koeleria macrantha*, *Helictotrichon*, *Aster alpinus*, *Potentilla acaulis*, *Artemisia commutata*)	Field climate manipulation	↓ Reproductive output	Liancourt *et al.* (2012)
Alpine grassland (*Deschampsia caespitosa*, *Anemone trullifolia*, *Potentilla anserine*, *Haplasphaera*, *Aster alpines*, *Gentiana formosa*, *Blymus sinocompressus*)	Field climate manipulation	↓ Reproductive output	Liu *et al.* (2012)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*)	Field climate manipulation	↑ Photosynthetic activity in cold periods	Llorens *et al.* (2003)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*)	Field climate manipulation	↑ Growth of *E. multiflora* and ↓ growth of *G. alypum*	Alla *et al.* (2012), Lloret *et al.* (2004a,b), Loe *et al.* (2005)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Boreal forest (*Picea abies*, *Populus tremuloides*)	Field observation	↑ Growth	Messaoud & Chen (2011)
Tundra (*Cassiope tetragona*, *Empetrum hermaphroditium*)	Field climate manipulation	↑ Growth	Michelsen *et al.* (1996)
Tundra (*Cassiope tetragona*, *Rannunculus nivalis*)	Field climate manipulation	↑ Reproductive output	Molau (1997)
Tundra (Papaver radicatum)	Field climate manipulation	↑ Growth	Molgaard & Christensen (1997)
Alpine grassland (*Cassia* and *Kobresia* species)	Field climate manipulation	↑ Growth	Na *et al.* (2011)
Tundra (*Eriophorum vaginatum*, *Carex bigelowii*, *Betula nana*, *Vaccinium ulginosum*, *Rubus chamamorus*, *Vaccinium vitis-idea*)	Field climate manipulation	↑ Growth	Natali *et al.* (2012)
Temperate grassland (*Lolium perenne*)	Field climate manipulation	↑ Growth	Nijs *et al.* (1996)
Temperate shrublands	Field climate manipulation	↑ Growth	Peñuelas *et al.* (2004a)
Temperate forest	Field observation	No significant growth changes	Peñuelas *et al.* (2008a,b)
Boreal, temperate and tropical forest	Field observation	No significant growth changes	Peñuelas *et al.* (2011a,b)
Alpine grassland (*Campanula rotundifolia*, *Acantium columbianum*, *Potentilla gracilis*, *Eriogonum subalpinum*, *Erigeron speciosus*)	Field climate manipulation	No significant growth changes related to decrease of soil moisture under warming	Price & Waser (2000)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*, *Pinus halepensis*)	Field climate manipulation	↑ Growth in *E. multiflora* and no effects in the other two species	Prieto *et al.* (2009a)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*, *Pinus halepensis*)	Field climate manipulation	↑ Photosynthetic activity	Prieto *et al.* (2009b)
Mediterranean and temperate shrublands	Field climate manipulation	↑ Growth	Prieto *et al.* (2009c)
Tundra, grasslands and forest	Review (meta-analysis) of 32 studies of field climate manipulation	↑ Growth	Rustad *et al.* (2001)
Tundra	Field climate manipulation	No effects on growth	Shaver & Jonasson (1999)
Mediterranean grassland	Field climate manipulation	↑ Growth	Shaw *et al.* (2002)
Alpine grassland (*Elymus nutants*, *Potantilla anserine*)	Field climate manipulation	↑ Growth of *E. nutants* and ↓ growth of *P. anserine*	Shi *et al.* (2010)
Tropical grassland (*Wedelia trilobata*, *Widelia chinensis*)	Field climate manipulation	↑ Growth	Song *et al.* (2010)
Tundra	Field climate manipulation	↑ Photosynthetic activity	Starr *et al.* (2008)
Alpine grassland (*Saxifraga oppositifolia*)	Field climate manipulation	No conclusive results on reproductive output	Stenstrom *et al.* (1997)
Temperate grassland (*Bromus sterilis*, *Chenopodium album*, *Senecio vulgaris*, *Bellis perennis*)	Greenhouse	↑ Growth	Stirling *et al.* (1998)
Nezara viridula	Lab experiment	↑ Reproductive output	Takeda *et al.* (2010)
Temperate forest (*Pinus nigra*)	Common garden	No effect on growth	Thiel *et al.* (2012)
Temperate grassland (*Lathyrus latifolius*, *Cerastium tomentosum*, *Artemisa verlotiorum*)	Common garden	↑ Growth	Verlinden & Nijs (2010)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Subtropical grassland (*Phalaris aquatic*)	Field climate manipulation	No conclusive results on growth	Volder *et al.* (2004)
Alpine shrubland and grass-shrublands (*Empetrum nigrum*, *Loiseleuria procumbens*)	Field climate manipulation	↑ Growth of shrublands and no effects or ↓ growth in shrub-grasslands	Wada *et al.* (2002)
Tundra (*Betula nana*, *Eriophorum vaginatum*, *Salix pulchra*, *Sphagnum species*, *Vaccinium species*, *Ledum decumbens*)	Field climate manipulation	↑ Growth in shrubs and ↓ growth in grasses	Wahren *et al.* (2005)
Tundra	Review of 11 field climate-manipulation experiments	↑ Growth of vascular plants and growth of nonvascular plants	Walker *et al.* (2006)
Temperate grassland (*Artemisa frigid*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, *Agropyron cristatum*)	Field climate manipulation	↑ Photosynthetic activity	Wan *et al.* (2009)
Temperate forest (*Acer rubrum*, *Acer saccharum*)	Field climate manipulation	↑ Growth production	Wan *et al.* (2004)
Temperate grassland	Field climate manipulation	↑ Growth in spring and autumn and ↓ growth in summer	Wan *et al.* (2005)
Boreal peatland (*Andromeda glaucophylla*, *Kalmia polifolia*)	Field climate manipulation	↑ Growth of shrubs and ↓ growth of grasses	Weltzin *et al.* (2003)
Temperate grassland (*Austrodanthonia caespitosa*, *Hypochaeris radicata*, *Leontodon taraxacoides*, *Themeda triandra*)	Field climate manipulation	↑ Growth of *A caespitose* and ↓ growth of *H. radicata* and *L. taraxacoides*	Williams *et al.* (2007)
All biome types	Meta-analysis of 85 sites with field climate manipulation	↑ Growth when not accompanied by a reduction in water availability	Wu *et al.* (2011a,b)
Temperate grassland	Greenhouse experiment	↑ Growth at short-term, but this response decreased progressively	Wu *et al.* (2012)
Semiarid grassland (*Artemisa frigida*, *Stipa ktylovii*, *Potentilla acaulis*, *Allium bidentatum*)	Field climate manipulation	No conclusive results on growth	Xia *et al.* (2009)
Alpine shrubland (*Cornicera hispida*, *Daphne refusa*)	Field climate manipulation	↑ Growth, no effects on reproductive output	Xu *et al.* (2009)
Alpine forest (*Abies faxoniona*, *Picea asperata*)	Field climate manipulation	↑ Growth and reproductive output	Yin *et al.* (2008)
Temperate grassland (*Ambrosia psilostachya*, *Helianthus mollis*, *Sorghastrum nutants*)	Field climate manipulation	↑ Photosynthesis in spring and ↓ photosynthesis in autumn	Zhou *et al.* (2007)

activity (Estiarte *et al*., 2008a) and turnover of fine roots (Wan *et al*., 2004). Most studies conducted in ecosystems not limited by water have thus observed increases in growth, photosynthetic activity and reproductive output of plants (Table 2). In tundra ecosystems limited by low temperatures, warming usually increases vascular plant growth and reduces nonvascular plant growth (Table 2), effects related to the increase in the availability of water (Clarke *et al*., 2012) and frequently limited by the availability of nutrients (Henry & Molau, 1997).

In contrast, plants under warming in dry areas respond to increased water deficits induced by associated increased evapotranspiration mainly by increasing their WUE (Brodribb & Hill, 1998; Peñuelas *et al*., 2008b) and generally by conservative mechanisms such as better control of photosynthetic capacity (Ogaya *et al*., 2011) and reduced growth (Table 2). A reduction in the availability of water has a negative effect on rubisco activity that limits CO_2 uptake (Flexas *et al*., 2004; Rennenberg *et al*., 2006). The physiological responses of plants to warming, therefore, range from changes that tend to increase plant production in cold-wet ecosystems to conservative responses that tend to increase the efficiency of use of resources in hot-dry ecosystems.

To complement these functional changes, plants can also alter their morphological structure to adapt to drought, mainly by increasing the allocation of carbon to the root system, thereby decreasing their stem/root ratio (Williams & Black, 1994; Xu *et al*., 2007; Meier & Leuschner, 2008; Shao *et al*., 2008; Dreesen *et al*., 2012), reducing their leaf size, increasing their leaf mass area (Ogaya & Peñuelas, 2006; Shao *et al*., 2008) and decreasing their leaf area index (Asner *et al*., 2004). The higher allocation of carbon to belowground tissues does not necessarily translate into a larger investment in mycorrhizal formation. Some studies have observed a trend of increasing investment in mycorrhizae (Shi *et al*., 2002), whereas others have observed the opposite trend (Staddon *et al*., 2004). The investment in mycorrhizal association under moderate drought can increase, but physiological stress limits the symbiosis at certain levels of drought (Shi *et al*., 2002).

Animals, particularly ectotherms, have several ways of physiologically adapting to warming. The most general and immediate responses in insects are an increase in metabolism and respiration (Neven, 2000) and the production of heat-shock proteins (Feder *et al*., 1997). When temperatures exceed a certain 'thermal limit', however, the number and intensity of the impacts on insect function threaten survival (Neven & Rehfield, 1995; Neven, 2000). Animals adapted to broad climatic gradients also have broad thermal tolerances and therefore respond better to the impacts of warming (Bonebrake & Deutsch, 2012). Moreover, spatial heterogeneity may play a critical role in thermal adaptation, particularly in the tropics where individuals can move to cooler or wetter parts of their current home ranges (Bonebrake & Deutsch, 2012) rather than altering their geographical distribution at the regional scale.

Growth and reproduction

Despite the observed phenotypic plasticity of plants in response to drought, a decrease in net production (Table 2) and reproduction (Ogaya & Peñuelas, 2007b) are the general responses of plants to drought. The intensities of these effects frequently differ among the species of a community (Peñuelas *et al*., 2004a; Ogaya & Peñuelas, 2007a,b; Wu *et al*., 2011a,b) and among the different levels of soil-water availability. A shift in phenology is one of the most conspicuous responses of plants and animals to current climate change (Körner, 1995; Peñuelas & Filella, 2001; Fitter & Fitter, 2002; Peñuelas *et al*., 2002, 2009b; Chuine *et al*., 2010) (Fig. 3). Climate warming has changed the life cycles of plants and animals, advancing the biological spring and delaying the arrival of biological autumn and winter (Peñuelas *et al*., 2002, 2009b; Badeck *et al*., 2004; Menzel *et al*., 2006; Steltzer & Post, 2009; Fridley, 2012). Several studies have observed significant advances in the timing of leaf expansion and flowering under warming in cold (Price & Waser, 1998; Thórhallsdóttir, 1998; Menzel & Fabian, 1999; Huelber *et al*., 2006), temperate (Peñuelas & Filella, 2001; Sherry *et al*., 2007; Rollinson & Kaye, 2012) and Mediterranean regions (Peñuelas & Filella, 2001; Peñuelas *et al*., 2002; Llorens & Peñuelas, 2005). In a meta-analysis of 125 000 observational series of 542 plant and 19 animal species in Europe, Menzel *et al*. (2006) observed that leaf unfolding had advanced 2.5 days per 1 °C of temperature increase, and leaf fall was delayed 1 day per 1 °C of temperature increase. Parmesan & Yohe (2003), in a review of available global data, reported an advance in leaf unfolding of 2.3 days per decade. These observations of advances in spring phases have been confirmed experimentally in the field in response to warming treatments of only about 1 °C (Llorens & Peñuelas, 2005; Prieto *et al*., 2009d). In most cases, though, the advances in these field experiments have been much lower than those observed in the field in recent decades (Wolkovich *et al*., 2012).

These effects, as those discussed earlier, vary for the different species of the community. For example, trees in temperate forests advance their leaf emergence to overlap with the period of emergence of the understory vegetation, thereby increasing competition (Rollinson & Kaye, 2012). Warming tends to advance flowering and fruiting in species that flower before the summer peak and delay flowering in species that flower after the

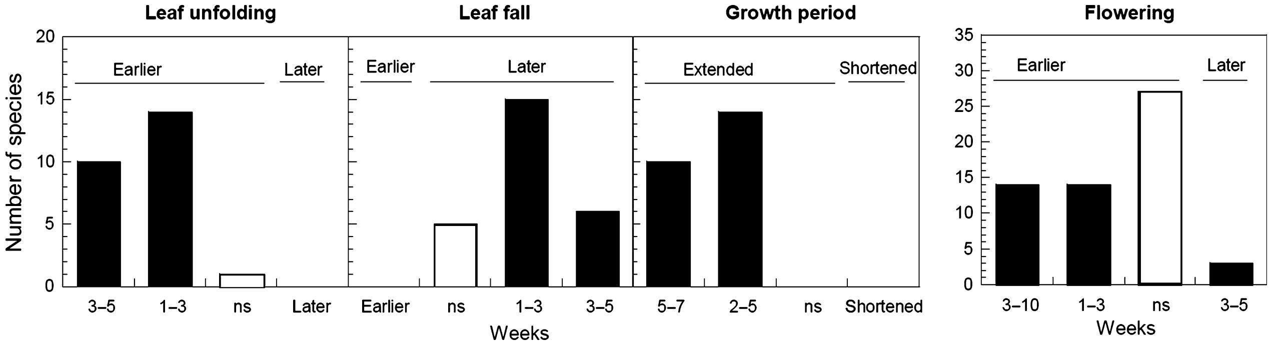

Fig. 3 Example of the phenological changes in the different species in the Montseny mountains (Catalonia, NE Spain) in the last 50 years of the 20th century. Based on Peñuelas *et al.* (2000a,b).

summer peak (Sherry *et al.*, 2007). Among the species that flower before the summer peak, the species that flower early tend to lengthen the duration of flowering by flowering earlier, whereas late-flowering species tend to advance the onset of flowering without increasing its duration (Giménez-Benavides *et al.*, 2011). These different shifts in plant phenology also produce a mismatch in species involved in the same biotic relationships, leading to disequilibrium in the sizes of populations (Both *et al.*, 2006). Mismatches have been singularly observed in mutualistic plant-pollinator relationships (Memmott *et al.*, 2007; Hoover *et al.*, 2012) and in plant–herbivore relationships (Post *et al.*, 2008; Green, 2010).

The specific phenological response of plants to drought has been less studied despite its important role (Peñuelas *et al.*, 2004b). Peñuelas *et al.* (2004b) found that the onset of greenup in the Iberian Peninsula shifts from spring (triggered by rising temperatures) in the northern cool-wet regions to autumn (triggered by the arrival of autumn rain) in the southern warm-dry regions. In water-limited ecosystems such as the Mediterranean ecosystems, experimental drier conditions (15–29% reduction in soil moisture) delayed the flowering period and decreased the number of flowers per plant (Ogaya & Peñuelas, 2004; Llorens & Peñuelas, 2005; Prieto *et al.*, 2008). This effect frequently had different intensities depending on the species in the studied community (Ogaya & Peñuelas, 2005). In contrast, in ecosystems of central Europe not limited by water, drought advanced the flowering period (Jentsch *et al.*, 2009). Because drought plays a key role in several parts of the world, intensive research on the phenological shifts it induces in plants and animals is warranted.

Warming also has significant direct effects on animal phenology by lengthening the period of summer activity and by increasing the number of reproductive cycles and larval size in insects (Stefanescu *et al.*, 2003; Harada *et al.*, 2005; Altermatt, 2010) or by changing the sex ratios in populations of turtles (Tucker *et al.*, 2008). In amphibians and birds, advanced periods of breeding and oviposition in response to warming have been observed (Beebee, 1995; Crick *et al.*, 1997; Schaefer *et al.*, 2006; Potti, 2009). An increase in reproductive success has been observed in reptiles (Zhang *et al.*, 2009; Takeda *et al.*, 2010; Clarke & Zani, 2012) and is frequently accompanied by an advance in the period of oviposition (Zhang *et al.*, 2009). Drought can have the opposite phenological effect to that of warming, for example, it has delayed phenological phases in butterflies of the Mediterranean basin (Stefanescu *et al.*, 2003).

The species-specific phenological responses of animals of the same community can be very different, with further consequences for biotic relationships (Stefanescu *et al.*, 2003). Guo *et al.* (2009), studying grasshoppers in Inner Mongolia, observed that the mid- and late-season species tended to advance the reproductive period, overlapping it with the early-season species, thus increasing the competition among different species of grasshoppers. In the Mediterranean Basin, with an expected increase in aridity, the varying degrees of phenological flexibility among species may account for differences in species' responses and, in the case of multivoltine species, strong selection is projected, favoring local seasonal adaptations such as diapauses or migratory behavior (Stefanescu *et al.*, 2003). In climates that are already warm, an enhanced warming can be important for ectothermic animals whose thermoregulative behavior can be critical for buffering the impact of severe warming (Kearney *et al.*, 2009).

The phenology of endothermic animals has also been affected by warming. The Alpine marmot has advanced its emergence from hibernation, leading to an earlier weaning of young and a longer growth season that thereafter imply larger body sizes before the next hibernation (Ozgul *et al.*, 2010). This larger body size favors a decline of adult mortality and a shift in the phenotypic composition of populations, which in turn triggers an abrupt increase in population size, thus showing that a phenological shift can cause sudden changes in evolution and demography (Ozgul *et al.*, 2010).

From individual changes to changes in populations, communities and ecosystems

The plasticity and degree of each individual to present intense responses at molecular, physiological, phenological and morphological levels are the first 'resources' to cope with the new climatic situation. Several studies, however, have observed that the responses of organisms are unable to prevent defoliation, decreases in growth, mortality, migration and shifts in the distributions of species (Peñuelas & Boada, 2003; Peñuelas *et al.*, 2007a,b, 2008b; Allen *et al.*, 2010; Carnicer *et al.*, 2011). Moreover, these responses at the level of individual organisms differ among individuals and species of the same community (Ogaya & Peñuelas, 2006; Volder *et al.*, 2010; Kardol et al., 2010; Ogaya *et al.*, 2011), implying further changes in community composition and feedback effects on climate change. We now discuss these impacts of climate change at the scales of populations, communities and ecosystems.

Responses of populations

Genotypic adaptation: microevolution

Plants can tolerate environmental changes '*in situ*' by a combination of phenotypic plasticity and genotypic adaptation (Jump & Peñuelas, 2005). The existence and magnitude of phenotypic plasticity, however, is under genetic control and is not unlimited (Jump & Peñuelas, 2005). Evidence suggests that phenotypic plasticity is submitted to strong selection pressure in the range limits of species distribution by the need of species communities to adapt to extreme conditions for the species (Fallour-Rubio *et al.*, 2009; Mátyás *et al.*, 2008). Phenotypic plasticity is thus likely to be under strong directional selection under climate change (Jump & Peñuelas, 2005).

Recent evidence links the genetic diversity of populations to population persistence in rapidly changing environments in wild ecosystems (Jump & Peñuelas, 2005; Eveno *et al.*, 2008; Jump *et al.*, 2008) (Fig. 4) and also relates genetic variability with climatic gradients (Elboutahiri *et al.*, 2010; Carnicer et al., 2012). Genomic approaches have become a potent tool for detecting alterations in population genetics (Luikart *et al.*, 2003; Storz, 2005; Bonin, 2008; Karrenberg & Widmer, 2008). With these techniques, the variation among individuals of the same population in the ability to establish under enhanced drought conditions has been observed in the Mediterranean shrub *Fumana thymifolia* (Jump *et al.*, 2008) and in *Pinus pinaster* (Eveno *et al.*, 2008). Direct rapid evolution toward drought avoidance was demonstrated in populations of *Brassica rapa*, where genotypes sampled after a multiyear drought showed significantly earlier flowering than did pre-drought individuals sampled from the same population (Franks *et al.*, 2007). Similarly, correlation between temperature and allele frequencies and directional changes in allele frequency in response to recent warming has been observed in populations of *Fagus sylvatica* (Jump *et al.*, 2006a). These and other similar examples suggest that, at least in some cases, climate-linked genotypic variation exists, and that plant species can respond to selection on a timescale relevant for responding to the current rapid anthropogenic environmental changes (Barrett & Schulter, 2008; Hoffmann & Willi, 2008; Jay *et al.*, 2012). This microevolutionary process has also been demonstrated in laboratory mesocosmic experiments studying the rapid microevolution of life-history traits (van Doorslaer *et al.*, 2007) and in field experiments where several loci presented significantly different frequencies in plants submitted to drought than in control plants (Jump *et al.*, 2008) (Fig. 4).

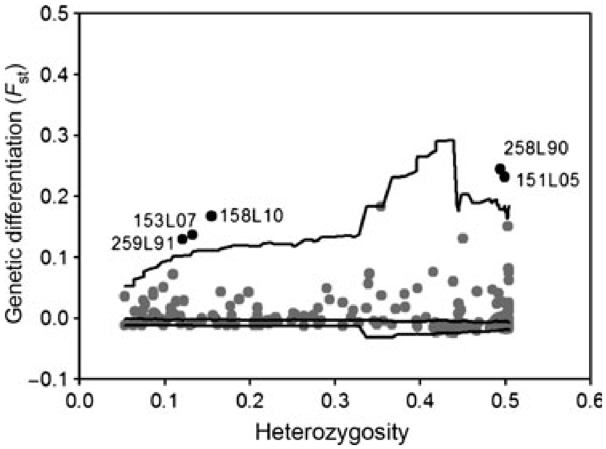

Fig. 4 Genetic differentiation between *Fumana thymifolia* individuals established in experimental drought and control treatments, based on AFLP molecular markers. The numbered loci are significantly more differentiated than would be expected if selectively neutral, indicating that selection resulting from elevated drought has resulted in changes in gene frequencies at these loci in the experimental treatment. Based on Jump *et al.* (2008).

Shifts in genetic composition in populations of birds are involved in recent changes in morphology and migration behavior related to climate changes (Pulido & Berthold, 2004). The presence of additive genetic variation within and among bird populations, and examples of rapid evolutionary responses to rare climatic events, suggest that birds also have a high potential for evolutionary change (Pulido & Berthold, 2004). Evolutionary adaptation can thus be rapid and can potentially help species to adapt to the current rapid changes in climate (Hoffmann & Sgrò, 2011), although the effectiveness of the evolutionary response to counter the negative impacts of rapid warming is generally expected to be rather more limited (Jump & Peñuelas, 2005).

Because different genotypes of the same species can differ in their functional traits in different environmental conditions, maintaining diversity within populations is likely to maximize the probability that the population will include the more adequate phenotypes in each different situation. Even though selection will lower the genotypic diversity of the population over time in a stable environment, gene flow and environment-dependent differences in fitness between genotypes interact with fluctuating selection pressures in a heterogeneous environment to maintain genotypic population diversity (Gutschick & BassiriRad, 2003). The loss of genetic variability elevates the vulnerability of populations to rapid environmental change (Esquinas-Alcázar, 2005; Hoffmann & Willi, 2008; Salvaudon *et al.*, 2008; Jump *et al.*, 2009a,b). Strong initial selection pressure in response to an environmental change, however, can also reduce genetic variability and the capacity of further adaptation if the environment continues to change (Newman & Pilson, 1997; Frankham, 2005; Leimu *et al.*, 2006; Endels *et al.*, 2007).

Despite the possible confusion between genotypic and plastic phenotypic responses in some studies, an increasing number of studies have observed signatures of rapid climate change on the microevolutionary response of populations (Gienapp *et al.*, 2008). The microevolution of a population in response to climate change is frequently related mainly to adaptation to altered seasonal events, such as drought or changes in seasonal length, rather than to the direct effect of a change in temperature (Bradshaw & Holzapfel, 2006). For example, in the study of *Brassica rapa* by Franks *et al.* (2007) referred to above, increases of multiyear droughts have induced microevolution in genotypes of *Brassica rapa* that has advanced the onset of flowering between 1.9 and 8.6 days relative to ancestral (predrought) phenotypes when both groups are grown under the same conditions.

Warming has impacts on insect populations living on the border of the species' distribution (Scriber, 2011). For example, in *hybrid zones* – the contact points between closely related and interfertile species, elevated genetic diversity and the disruption of gene complexes through recombination between different but genetically proximate species can open the way to rapid adaptation and speciation in response to environmental changes (Scriber & Ording, 2005; Scriber, 2011). The faster and more frequent shifts in species distributions under climate change can increase this type of speciation, potentially helping populations to adapt to changes in environmental gradients (Scriber, 2011).

Future studies should expand our knowledge of the interplay between plastic phenotypic, genotypic and epigenetic changes in the adaptation of organisms to current climate change (Hedhly *et al.*, 2008). Further research is required to identify both appropriate short- and long-term data sets for a range of species, traits and suitable analytical methods, which will permit the study of the complex interaction between phenotypic plasticity and genetic adaptation of organisms and their populations in response to climate change. Climate change constitutes an outstanding opportunity for genetic and evolutionary ecologists to advance our knowledge of the links, tuning and trade-offs among phenotypic plasticity, genotypic variability and population structure in the evolutionary success of species.

Changes in distribution and migration

There is accumulating evidence of changes in the distribution of organisms in response to climatic changes. In plants, the shifts currently most widely observed are those due mainly to drought interacting with hot summers that increase the limitation of water and erode the trailing range edge populations of a species, resulting in a contraction of its distribution toward wetter and cooler higher latitudes and altitudes (Pigott & Pigott, 1993; Allen & Breshears, 1998; Colwell *et al.*, 2008; Kullman, 2008; Jump *et al.*, 2009a,b; Harrison *et al.*, 2010) or due to elevated temperatures that allow population expansion at the leading range edge (Walther, 2003; Peñuelas *et al.*, 2007a,b; Kullman, 2008; Crimmins *et al.*, 2009; Jump *et al.*, 2009a,b). Range shifts, therefore, occur due to the combination of population expansion at the leading edges of distributions, through increased reproduction and establishment, and retraction at the trailing edges driven by elevated mortality and declines in growth and reproduction (Allen & Breshears, 1998; Peñuelas & Boada, 2003; Jump *et al.*, 2006a,b, 2007, 2009a; Peñuelas *et al.*, 2007a,b; Colwell *et al.*, 2008; Worrall *et al.*, 2008). More favorable climatic conditions can produce a shift in plant populations within the same altitudinal level across different montane aspects, from unfavorable to the most favorable climatic conditions resulting from differences in the hours of direct sunlight (Diemer, 2002). However, under more favorable climatic conditions for survival, range expansions are not inevitable as the shifting of the leading edge also depends on biotic factors such as herbivore pressure (Munier *et al.*, 2010) and dispersal dynamics (Fordham *et al.*, 2012).

Although distributional shifts are predicted along both latitudinal and altitudinal gradients, several physical and climatic factors have different patterns of variation in altitude than in latitude, such as partial CO_2 pressures and UV radiation. Furthermore, the physical distance necessary to reach sites with significantly different temperatures and/or pluviometry is measured in meters in altitude as opposed to similar changes occurring over kilometers along latitudinal transects (Körner, 2007). The isolation of populations of once widespread species and their retention in locally favorable sites can result in the formation and persistence of relict populations. In both lowland and mountainous areas, the presence of local variations in soil, microclimate and topographic heterogeneity, despite regionally unfavorable climates, can increase the resilience and resistance of local populations despite wider population declines (Ashcroft *et al.*, 2009; Godfree *et al.*, 2011; Hampe & Jump, 2011). Such increased isolation can also increase population divergence, resulting in the independent evolution of populations of a formerly more cohesive distribution (Jump & Peñuelas, 2005, 2006).

In animals, an increasing number of studies have shown changes in species distributions related to warming and drought (Guo *et al.*, 2009; Lenoir *et al.*, 2010; Kocsis & Hufnagel, 2011). Because of their higher mobility, animals have a greater capacity than plants to escape unfavorable climatic conditions. Despite the capacity of ectothermic animals such as insects to adapt, they present a 'heat-scape' temperature, described as the temperature that drives the insect to leave a site (Ma & Ma, 2012). This temperature differs among species of insects, suggesting that the composition of species communities under warming can change largely because of the different rates of migration of the different species (Ma & Ma, 2012). Changes in migration at regional scales have been observed in some groups of insects. For example, in butterflies, poleward shifts associated with regional warming have been observed in some species in Europe (Parmesan *et al.*, 1999).

In vertebrates, the rates of migration within a species sometimes differ with genotype, favoring the possibility of allopatric speciation such as observed in populations of the lizard *Lacerta vivipera* (Lepetz *et al.*, 2009). Birds can migrate in response to other human-driven effects, such as changes in land use, and/or by changes in biotic relationships related to warming (Lenoir *et al.*, 2010). However, the controversy over whether or not the changes in migratory behavior, for example in the long-distance migration of birds, are due to genotypic evolution remains (Both, 2007). Finally, the number of limitations and constraints of latitudinal shifts are large, from geographic natural barriers and lack of adequate food sources to human-driven constraints such as urbanization and habitat conversion (Jump *et al.*, 2009a, b). Consequently, and due to both natural and anthropogenic causes, each of these altitudinal and latitudinal shifts in plant species has its own peculiarities such that individual rates of migration will have impacts at the level of the community (Huntley, 1991).

Mortality and local extinction

Disturbance of species interactions, together with the low probability that phenotypic, genotypic and migrational responses will allow most species to tolerate rapid climate change, suggest a range-wide increase in individual mortality (Peñuelas *et al.*, 2000b) and therefore in the risk of local extinction (Jump & Peñuelas, 2005).

Furthermore, extreme temperatures in summer, which further exacerbate drought, increase dieback and reproductive failure in large areas on a continental scale (Peñuelas *et al.*, 2000b; Saxe *et al.*, 2001; Breshears *et al.*, 2005; Körner, 2007; Fensham *et al.*, 2009; Peng *et al.*, 2011). These dieback events by extreme climate changes are occurring with increasing frequency worldwide (Allen, 2009; Allen *et al.*, 2010). The threat of local extinction is even higher for species living in sites with restrictions to geographic shifts of populations toward more favorable areas, such as the higher altitudes of mountains (Rull & Vegas-Vilarrubia, 2006; La Sorte & Jetz, 2010), but this threat can be buffered by the presence of high topographic variability that allows suitable microclimates or sites with suitable soils (Peñuelas *et al.*, 2000b; Ashcroft *et al.*, 2009; Scherrer & Körner, 2011).

Defoliation and dieback thus increase when the phenotypic and genotypic capacity and the capacity of population movement are insufficient to cope with the climate change (Ogaya & Peñuelas, 2007a; Carnicer *et al.*, 2011) (Fig. 5). The consequenses of exceeding such tolerance thresholds are evident from historical data in the Mediterranean area showing substitution of forest by shrublands and deserts in relatively short periods of time (Estiarte *et al.*, 2008b) (Fig. 6).

Particular traits of species can render some species especially resistant or vulnerable to the risk of extinction. For example, *Phillyrea latifolia* can withstand warming and drought in Mediterranean forests much better than *Quercus ilex* because it dissipates excess radiation better and has stronger hydraulic resistance and higher WUE (Peñuelas *et al.*, 1998, 2000a,b). In another example, Iszkulo *et al.* (2009) have observed a

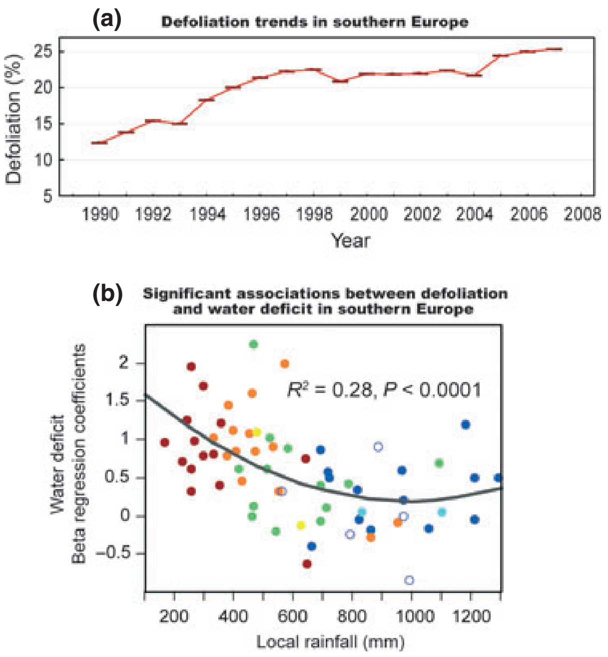

Fig. 5 (a) Increased defoliation in southern European forests in recent decades. (b) Defoliation in the Iberian Peninsula modeled as a function of water deficit (Emberger index) in generalized linear mixed models for each tree species in areas of different mean annual rainfall (i.e., rainfall quantiles). Significant coefficients of regression (β values) between water deficit and defoliation are plotted. The red dots represent beta values for 0–25 rainfall quantiles; orange dots, 25–50 quantiles; yellow dots, 0–50 quantiles; green dots, 50–75 quantiles; dark-blue dots, 75–100 quantiles; light-blue dots, 50–100 quantiles; white dots, species of restricted geographical distribution. Based on Carnicer *et al.* (2011).

large intolerance to drought in females of *Taxus baccata*, which strongly reduces the reproductive success of the species and makes it especially vulnerable to extinction in areas under increased drought.

Highly diverse ecosystems are sensitive to losses of biodiversity in response to warming and drought (van Peer *et al.*, 2004). Because of their high biodiversity, tropical forests particularly suffer from the impacts of the current rapid climate change. Moreover, a reduction in the availability of water has a large impact on tropical forests because of the long-term adaptations of their organisms to high temperatures and availability of water. Current models project a high risk of losses of biodiversity in tropical forests by warming (Malcolm *et al.*, 2005). In the dry tropical forests of Central America, a rapid increase in drought by the lengthening of the drought season by 4 weeks can cause the extinction of 25–40% of forest species (Condit, 1998). Sensitivity may also be high in temperate or boreal systems of low diversity, however, when dieback occurring in the two main species forming the canopy may generate strong transformations at the ecosystemic scale, from forest to shrubland, for example.

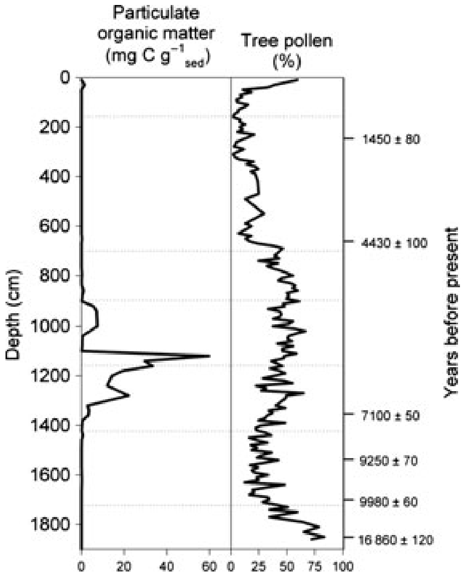

Fig. 6 Changes in the land cover from forest to shrubland in southern Spain in the last millennium. Based on Estiarte *et al.* (2008b).

Elevated temperatures can directly threaten the survival of populations by restricting migration to higher altitudes (Shoo *et al.*, 2005). Populations of tropical animals, particularly of ectotherms such as insects and reptiles, are especially threatened under warming because they currently live very close to their optimal temperatures. Those species that live in sites with limited possibilities for migration, such as mountainous areas or islands, have a high risk of local extinction (Chiu *et al.*, 2012).

Changes in communities

Through changes in abiotic factors

Apart from drought and warming themselves, one frequently observed abiotic effect of climate change is the shift in availability of soil nutrients (Hobbie & Chapin, 1996; Shaver *et al.*, 2000; Schmidt *et al.*, 2002; Beier *et al.*, 2008; Li *et al.*, 2011d; Sardans *et al.*, 2012b). Because organisms frequently respond to climate change by shifting their chemical composition and use of resources (Sardans *et al.*, 2012b), they can exert an effect on ecosystemic C, N and P cycles that thereafter can produce feedback effects on the community species that must respond to these cycles (Finzi *et al.*, 2011). Drought decreases the activities of soil enzymes (Garcia *et al.*, 1994; Sardans & Peñuelas, 2005, 2010; Sardans *et al.*, 2008b,c) and the turnover and availability of nutrients (Sardans & Peñuelas, 2004, 2007; Bloor & Bardgett, 2012), effects that generate changes in the elemental composition of plants that vary in intensity in the different species of the plant community (Sardans *et al*., 2007; Peñuelas *et al*., 2008a). For example, a relative increase in fungal vs. bacterial dominance in soil communities has been repeatedly reported in response to drought (Yavitt *et al*., 2004; Yuste *et al*., 2011).

In cold and wet temperate areas, warming frequently increases the decomposition of soil organic matter (Schmidt *et al*., 2002; Wessel *et al*., 2004; Gornall *et al*., 2009; Butler *et al*., 2012), availability of soil nutrients (Beier *et al*., 2008; Aerts, 2010), plant growth (Molau, 1997; Hill & Henry, 2011) and biomass of the soil community and leads to changes in its species composition (Sjursen *et al*., 2005; Zhang *et al*., 2005b; Schulte *et al*., 2008; Yergeau *et al*., 2012) . These changes provide new competitive scenarios both among plants (Gornall *et al*., 2009) and between plants and microbes (Schmidt *et al*., 2002).

Warming can also change the relationships of interspecific competition by changing the structure of the physical habitat. For example, sympatric species of penguins have changed their competitive equilibrium as a result of a reduction in the extent of sea ice produced by warming, which has a greater detrimental effect on species that depend on ice area for their reproduction and fishing (Forcada *et al*., 2006).

Through biotic effects on the structure and function of trophic webs

The direct effects of climate change on the different species of a community also change the biotic relationships among the species. Species must therefore adapt to new scenarios of competitive and trophic relationships.

Warming can exert a direct effect on the relationships of interspecific competition because plant species of the same community frequently respond with different intensities in both their growth and their reproduction (Shaver *et al*., 2000; Weltzin *et al*., 2000, 2003; Walker *et al*., 2006; Williams *et al*., 2007; Prieto *et al*., 2009b; Green, 2010; Verlinden & Nijs, 2010; Bokhorst *et al*., 2008, 2011; Messaoud & Chen, 2011; Zhang *et al*., 2011b; Reed *et al*., 2012). In some cases, the increases in growth of some species are accompanied by decreases in growth in other species (Day *et al*., 1999; Price & Waser, 2000; Cornelissen *et al*., 2001; Walker *et al*., 2006; Gebler *et al*., 2007). These asymmetrical effects are further related to competitive suppression (Kudo & Suzuki, 2003; Reed *et al*., 2012) and decreases in the diversity of species in plant communities (Farnsworth *et al*., 1995; Cornelissen *et al*., 2001; Klein *et al*., 2004; Walker *et al*., 2006; Cross & Harte, 2007; Gedan & Bertness, 2009; Prieto *et al*., 2009d; Lang *et al*., 2012a). Some groups, for example lichens, are more prone to extinction in cold areas submitted to warming (Wahren *et al*., 2005; Walker *et al*., 2006). The loss of biomass from the disappearance of some species is frequently compensated by an increase in growth of the remaining species (Cross & Harte, 2007). For example, the loss of biomass and diversity in lichens of arctic ecosystems is related to increases in the biomass and diversity of shrubs and herbs (Wahren *et al*., 2005; Walker *et al*., 2006; Joly *et al*., 2009). Warming increases interspecific competition and discourages the establishment of new plant species, especially when the community is highly diverse (Klanderud & Totland, 2007) potentially limiting population expansion for some species.

Warming has bottom-up effects. The plant–herbivore relationship is one of the most important biotic relationships. It depends on the coordination between plant and herbivore phenology (Loe *et al*., 2005). Outbreaks of insects are likely to increase under global warming due to the direct effects of higher temperatures on these ectothermic animals (Tobin *et al*., 2008; Jönsson *et al*., 2009) and to the extension of their active periods (Tobin *et al*., 2008; Jönsson *et al*., 2009). The changes in phenology and distribution caused by warming can also asymmetrically affect herbivores and predators (Barton, 2010); predators can compensate for the decrease in encountering herbivores by increasing their activity (Lang *et al*., 2012b). Some long-term field and laboratory studies suggest that warming disproportionally affects the loss of top predators and herbivores compared to autotrophs and microbes (Petchey *et al*., 1999).

A paradigmatic case of indirect biotic alteration resulting from the effects of warming on plant and animal metabolism is that produced by the increase in biogenic volatile organic emissions (BVOCs). This increase varies depending on the plant (and animal) species and the phenological and ontogenic stage, but it is also different for the hundreds or thousands of different BVOCs emitted by plants. As a result, significant changes occur in the protection of plants from climatic stresses, the communication between plants and pollinators, the relationships among plants and with herbivores and the defense of plants from pathogens, among others (Peñuelas & Staudt, 2010; Llusia *et al*., 2010, 2011) (Fig. 7). Significant changes in the competitive abilities of species are highly likely to result in changes in the composition of communities (Peñuelas & Staudt, 2010).

Warming can also exert indirect effects on communities by top-down mechanisms. Warming can increase the activities of predators and change hunting strategies between pursuit and wait/ambush, which changes the competitive pressures on different species of predator and drives some to extinction (Barton & Schmitz,

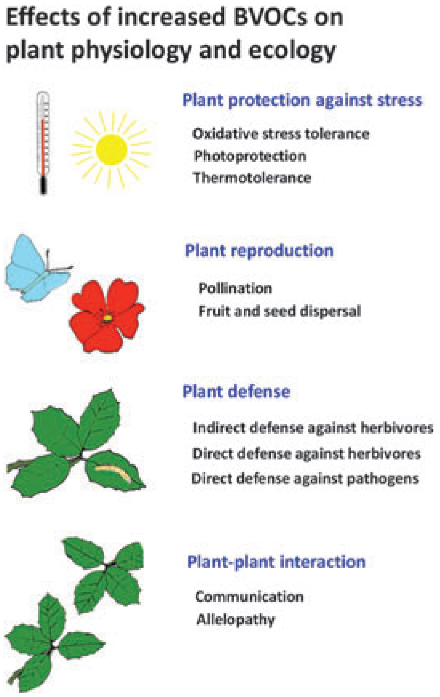

Fig. 7 Flow-on effects of warming on community processes through changes in plant BVOC emissions. Based on Peñuelas & Staudt (2010).

2009). Increases in herbivore pressure can have complex effects on community structure as increases in herbivore activity under warming are frequently asymmetrical, with most herbivores increasing their activity while others decrease theirs (Rizhsky *et al*., 2004). Populations of bark beetles in the boreal forests of Canada have grown because the number of stressed and ill trees, which are sources of food for these herbivores, have increased under warming, a situation that impacts the entire boreal community (Choi, 2011). A higher activity of herbivores can asymmetrically impact different plant species and thus change the scenarios of competition among them (Van Bogaert *et al*., 2009). The gregarious behavior of North American wolves in some areas varies depending on the intensity of winter snow. In years with more snow, wolves hunt more efficiently in large groups and can triple the number of deer killed compared to years with less snow when the wolves hunt in smaller groups. Deer populations thus rise in years with less snow, and the understory of the fir forest decreases, whereas contrary top-down effects occur in years with high snow cover (Post *et al*., 1999). The decreases in understory vegetation generated by a high presence of deer in years of low snowfall also decrease the populations of songbirds (Martin & Maron, 2012).

Drought can also change the competitive relationships in arid areas because the capacities and strategies of plant species to adapt to drought are different, as reported in several observational and experimental studies (Llorens *et al*., 2003; Ogaya & Peñuelas, 2003, 2005, 2006, 2007a; Lloret *et al*., 2004a,b; Loe *et al*., 2005; Ripley *et al*., 2010; Belerkuhnlein *et al*., 2011). In this new scenario of plant interspecific competition, species less able to adapt to drought can be eliminated. Long-term experimental studies are needed to determine whether species whose production, flowering or growth are negatively impacted by drought have compensatory mechanisms, for example by enhancing their defensive capacity against herbivores or their competitive ability against neighboring plants through chemical allelopathy. Compensatory mechanisms can help these initially disfavored species to remain, perhaps with lower density, in their current ranges under drought conditions. Plant defenses such as phenolics increase under warming (Scriber, 2011) and drought (Hale *et al*., 2005; Atala & Gianoli, 2009) and can then act as deterrents to herbivores (Eichhorn *et al*., 2007; Cipollini *et al*., 2008). Drought frequently has bottom-up effects that impact on plant cover and reduce species richness (Tilman & Haddi, 1992; Lloret *et al*., 2004b, 2009; Yurkonis & Meiners, 2006; Reed *et al*., 2012). Drought reduces the quality and abundance of host plants, thereby reducing herbivore populations (Sumerford *et al*., 2000) and affecting the entire trophic web (Sumerford *et al*., 2000; Pritchard *et al*., 2007). Drought can also have strong top-down effects. In Mediterranean regions, drought has been related to the loss of insect species, especially of specialist insects (Stefanescu *et al*., 2011). The trade-offs between defenses to drought and to herbivores remain unclear but seem quite variable (Haugen *et al*., 2008; Gutbrodt *et al*., 2012).

Ecosystems

Climatic feedbacks

When changes in phenology and plant communities are large, at regional and continental scales, they can exert significant feedback effects on climate (Peñuelas *et al*., 2009b) (Fig. 8). Lengthening the period of plant activity can increase the uptake of atmospheric CO_2 (Peñuelas & Filella, 2001), thereby buffering the increased levels of CO_2. Despite the lengthening of plant activity, the increase in frequency and severity of drought seems to have precluded the expected increase in tree growth worldwide (Peñuelas *et al*., 2011a,b) and in the fixation of CO_2 (Angert *et al*., 2005; Ciais *et al*., 2005; Buermann *et al*., 2007; Zhao & Running, 2010). The emissions of plant BVOCs also increase with temperature and longer periods of plant activity (Peñuelas & Llusia, 2003; Peñuelas *et al*., 2005; Blanch *et al*., 2007, 2011) (Fig. 8). Although their atmospheric lifetime is short, BVOCs have an important influence on climate through the formation of aerosols that can cool the Earth's surface during the day by intercepting solar radiation (Claeys *et al.*, 2004; Kullman, 2008) (Fig. 9). Moreover, a longer presence of green cover should influence other factors such as albedo, latent and sensible heat and atmospheric turbulence (Peñuelas *et al.*, 2009b). In some areas of North America, spring temperatures are different after leaf emergence due to increases in latent heat (Schwartz, 1996; Fitzjarrald *et al.*, 2001). Moreover, the denser the cover, the higher the turbulence and latent heat, leading to a cooler and wetter atmospheric boundary layer (Bonan, 2008). Increasing the duration of green cover can thus generate a cooling by sequestering more CO_2 and by increasing evapotranspiration. On the other hand, higher plant production and increased evapotranspiration decrease soil moisture and may generate abrupt rises of temperature when drought precludes evapotranspiration. An early and prolonged green period with increased evapotranspiration may have enhanced recent summer heat waves in Europe by lowering soil moisture (Zaitchik *et al.*, 2006; Fisher *et al.*, 2007). Decreases of soil moisture have a negative effect on late cooling and consequently increase surface temperature (Fisher *et al.*, 2007) and probably reduce summer precipitation (Jentsch *et al.*, 2009).

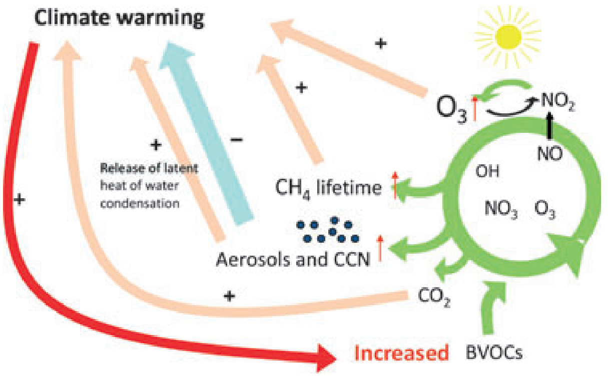

Fig. 8 Flow-on and feedback effects of warming on atmospheric processes through changes in plant BVOC emissions. Based on Peñuelas & Staudt (2010).

All these feedbacks generated by the lengthening of the period of plant growth are also generated by permanent changes in communities and ecosystems that also change the vegetative cover. For example, the shifts from forest to shrubland or to grassland described above as responses to climate change (e.g., Estiarte *et al.*, 2008b) must have significant biophysical (albedo, latent heat, sensible heat) and biogeochemical (e.g., decreased CO_2 fixation, changed BVOC emission, altered exchanges of greenhouse gases) feedbacks (Bonan, 2008).

One of these feedbacks, which may be the key feedback affecting climate change, is the changing role of ecosystems in the fixation of CO_2. We have yet to discern whether the current widespread summer droughts negate the enhancement of CO_2 uptake induced by

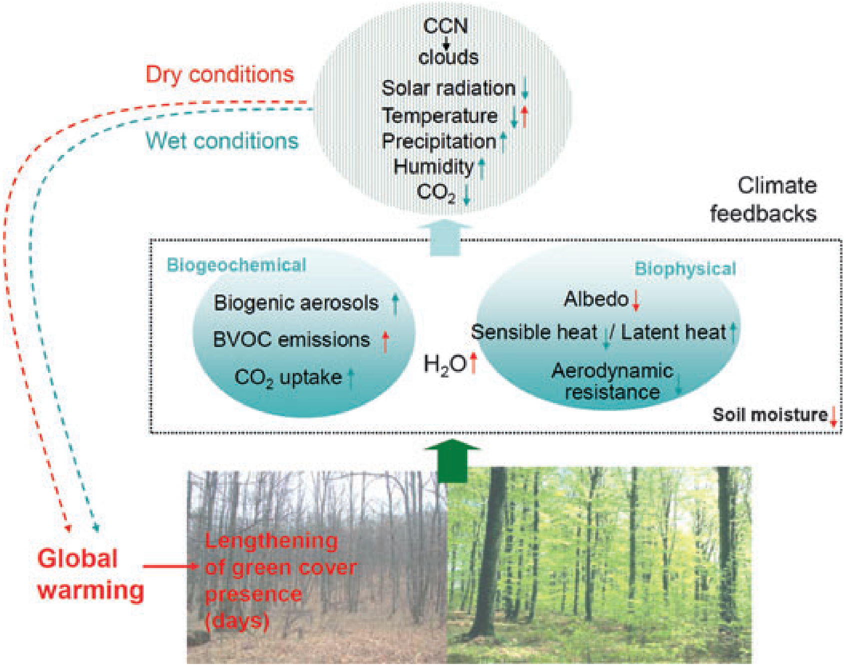

Fig. 9 Feedbacks on climate of the lengthening of the growth period in response to global warming. Based on Peñuelas *et al.* (2009a).

warmer springs, possibly by CO_2 fertilization or increased eutrophication. An accurate continuous quantification of the role of ecosystems as carbon sinks and the changes produced by climate change constitutes a key issue in the face of ongoing disturbance. Current tools for the continuous monitoring of carbon uptake by ecosystems include eddy covariance and remote sensing. Eddy covariance is currently the only direct way to assess the carbon flux of whole ecosystems with high temporal resolution. Nevertheless, towers for eddy covariance can effectively measure a single 'point' over flat and uniform terrain, usually on a scale of a few square kilometers or less (Baldocchi, 2003). Remote sensing has, instead, the ability to extend the spatial coverage of observations of carbon flux beyond a fixed point. Promising approaches include the use of the Photochemical Reflectance Index (PRI) (Garbulsky *et al*., 2011; Peñuelas *et al*., 2011a,b) or of fluorescence (Frankenberg *et al*., 2011) that offer good prospects for the continuous global monitoring of plant primary productivity from space (Fig. 10).

Conclusions and perspectives for future research

These many lines of evidence indicate that current climate change is having a great impact on organisms, populations, communities and terrestrial ecosystems by changing phenotypes, genotypes, growth, phenology, the distribution of organisms, species competitive ability, ecological relationships and the risk of extinction in communities. Ecosystems are thus changing in structure and function and have significant feedbacks on climate change itself.

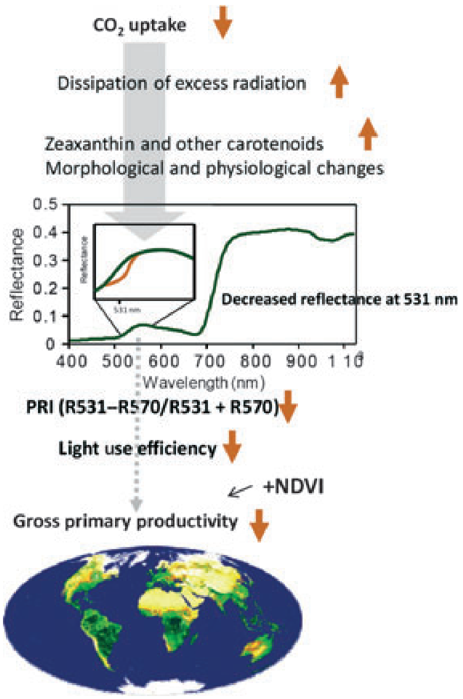

Fig. 10 Photochemical Reflectance Index (PRI) as a possible monitor of gross primary productivity everywhere all the time. Based on Peñuelas *et al.* (2011b). NDVI Normalized difference vegetation index or similar index providing a proxy of absorbed radiation by green biomass.

We know less about how these primary responses affect the capacity of organisms, populations, communities and ecosystems to respond to the interactions with the other simultaneous stresses produced by other drivers of global change and to the new biotic relationships that are generated. As one example among many of the interactions from global change, the current changes in the N : P ratios of organisms and environments, which some ecosystems are experiencing as a result of the unbalanced input to the biosphere by humans (Peñuelas *et al*., 2012), can strongly interact with climate change. We can hypothesize that in a scenario of drought, an increase in the N : P ratio can interact with the decrease in the availability of water, favoring species with low rates of growth and more conservative uses of resources. The N : P ratios can significantly affect the rate and direction of the responses of organisms, populations and communities to climate change, but no information about this possibility is available.

Current studies of field climatic manipulations interacting with eutrophication or elevated levels of CO_2, though, can help. They should continue as long as possible as many lines of evidence indicate that the longer in time and the wider in space the experiments are conducted, the more buffered are the changes described (Leuzinger *et al*., 2011). They must also be complemented with observational studies based on inventories (Carnicer *et al*., 2011), remote sensing data (Zhao & Running, 2010), paleoecological data (Estiarte *et al*., 2008b) and large data sets (Kattge *et al*., 2011) to shed light on the actual impacts climate change is having on life on Earth. The coupling of omic studies with studies of nutrient cycles, nutrient availability and stoichiometry, physiological and phenological changes and ecosystem structure shifts will allow making a step forward on our integrated understanding of the mechnisms and processes underlying biological impacts of climate change.

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