

Latitudinal gradients as natural laboratories to infer species' responses to temperature

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Summary

1. Macroclimatic variation along latitudinal gradients provides an excellent natural laboratory to investigate the role of temperature and the potential impacts of climate warming on terrestrial organisms.

2. Here, we review the use of latitudinal gradients for ecological climate change research, in comparison with altitudinal gradients and experimental warming, and illustrate their use and caveats with a meta-analysis of latitudinal intraspecific variation in important life-history traits of vascular plants.

3. We first provide an overview of latitudinal patterns in temperature and other abiotic and biotic environmental variables in terrestrial ecosystems. We then assess the latitudinal intraspecific variation present in five key life-history traits [plant height, specific leaf area (SLA), foliar nitrogen:phosphorus (N:P) stoichiometry, seed mass and root:shoot (R:S) ratio] in natural populations or common garden experiments across a total of 98 plant species.

4. Intraspecific leaf N:P ratio and seed mass significantly decreased with latitude in natural populations. Conversely, the plant height decreased and SLA increased significantly with latitude of population origin in common garden experiments. However, less than a third of the investigated latitudinal transect studies also formally disentangled the effects of temperature from other environmental drivers which potentially hampers the translation from latitudinal effects into a temperature signal.

5. *Synthesis.* Latitudinal gradients provide a methodological set-up to overcome the drawbacks of other observational and experimental warming methods. Our synthesis indicates that many life-history traits of plants vary with latitude but the translation of latitudinal clines into responses to temperature is a crucial step. Therefore, especially adaptive differentiation of populations and confounding environmental factors other than temperature need to be considered. More generally, integrated approaches of observational studies along temperature gradients, experimental methods and common garden experiments increasingly emerge as the way forward to further our understanding of species and community responses to climate warming.

Key-words: altitudinal gradients, climate change, common garden experiments, experimental warming, functional life-history traits, global warming, latitude, plant–climate interactions, transplant experiments

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Introduction

Our planet is warming significantly: the global mean annual temperature was 0.8 °C higher during the last decade (2000s) than at the beginning of the twentieth century (Hansen *et al.* 2010). Compared with this global mean, the warming trend was 50% higher in the United States, two to three times higher in Eurasia and three to four times higher in the Arctic (Hansen *et al.* 2010). Temperature is a major determinant of the physiology, fitness and distribution of organisms (Woodward 1987), and climate warming is thus expected to have profound consequences on biodiversity and ecosystem functioning (Lovejoy & Hannah 2005).

Two main approaches are available to empirically examine the effects of warming on terrestrial organisms: (i) monitoring the response of organisms to temporal or spatial temperature variation, for example, across years, altitudes and/or latitudes (Koch *et al.* 1995; Körner 2003, 2007; Ibáñez *et al.* 2007; Lenoir *et al.* 2008; Reich & Oleksyn 2008), and (ii) performing experiments with warming facilities such as infrared heaters, open-top chambers, soil heating cables or glasshouses (Kimball 2005; Walker *et al.* 2006; Bokhorst *et al.* 2011; Wolkovich *et al.* 2012). Each of these approaches is associated with specific advantages and drawbacks. Studies exploiting interannual temperature variability are powerful to better understand temperature effects on local population dynamics (e.g. Clark *et al.* 2003; Ibáñez *et al.* 2007), but their results are difficult to extrapolate temporally and spatially due to the confounding effects of factors such as local adaptation, species interactions and differences among historic, current and future climate change (Dunne *et al.* 2004). Likewise, experimental warming facilities enable researchers to dissect temperature effects from other confounding environmental factors that covary with temperature in natural conditions, as is the case in gradient studies. In an experiment, it is also possible to study organisms' responses to temperature values or patterns yet not occurring under natural conditions, such as predicted extreme temperatures. However, these experimental studies are typically performed at smaller spatial and/or temporal scales, the data are often obtained with a step-increase in temperatures, and experiments can disturb other abiotic conditions including light availability, CO₂ concentration, relative air humidity, wind speed and soil moisture content, or biotic interactions such as pollination and herbivory (Kimball 2005; Rustad 2008; Aronson & McNulty 2009; De Boeck, De Groot & Nijs 2012; Wolkovich *et al.* 2012). These unintended disturbances in experimental settings can result in, for instance, the underprediction of phenological responses to warming as detected in observational studies (Wolkovich *et al.* 2012; but see Harte & Kueppers 2012).

Studies comparing populations across sites with contrasting temperatures, such as altitudinal and latitudinal gradients, can provide invaluable information about the role of temperature on the structuring and functioning of ecosystems. Mostly, for methodological reasons (Jump, Mátyás & Peñuelas 2009), latitudinal gradients have been used much less as natural laboratory to assess responses of terrestrial organisms to climate warming than altitudinal gradients. Illustratively, a number of studies have reported recent altitudinal range shifts of plants

(e.g. Beckage *et al.* 2008; Kelly & Goulden 2008; Lenoir *et al.* 2008; le Roux & McGeoch 2008; Parolo & Rossi 2008; Bertrand *et al.* 2011; Crimmins *et al.* 2011; see Jump, Mátyás & Peñuelas 2009 for an overview), while fewer have described latitudinal shifts (Lescop-Sinclair & Payette 1995; Sturm, Racine & Tape 2001; Zhu, Woodall & Clark 2012). The relative lack of studies using latitudinal gradients as natural laboratories merits attention given the different abiotic and biotic processes occurring along both types of spatial gradients. For instance, the spatial rate of temperature change is much higher when moving up in elevation than across latitudes (Jump, Mátyás & Peñuelas 2009). As a result, the 'velocity of climate change' (i.e. the velocity [km year⁻¹] one needs to travel with from site A to site B to maintain constant temperatures over time) is much greater along latitudinal than altitudinal gradients (Loarie *et al.* 2009) which may result in higher lags behind climate warming in terms of species migration or community shifts (Bertrand *et al.* 2011). Additionally, the smaller geographical distances typically involved in altitudinal gradients imply different levels of gene flow between populations. As a result, patterns of genetic differentiation and local adaptation are expected to differ along latitudinal and altitudinal transects (Davis & Shaw 2001; Jump, Mátyás & Peñuelas 2009). Auxiliary data may then be required to determine how much of the observed phenotypic differences are due to plastic responses versus adaptive differentiation between populations. Thus, altitudinal and latitudinal gradients differ in a number of factors that could be responsible for divergent species responses observed across both types of spatial gradients. As sites along a latitudinal gradient have evolved with the local climate over centuries, they provide a unique additional opportunity to assess the integrated long-term effects of temperature on terrestrial organisms in a larger ecosystem framework (Rustad 2008). Such an approach is likely to provide complementary insights to studies based on altitudinal transects, local interannual variability or experimental manipulations.

Here, we review the use of latitudinal gradients as natural laboratories to study climate-warming impacts on biota. While our review is generally applicable to terrestrial organisms, we pay particular attention to vascular plants. First, we provide an overview of the existent latitudinal variation in temperature as well as of covarying abiotic and biotic environmental variables, which can confound analyses across latitudes. We then quantify latitudinal intraspecific variation present in five key plant functional traits with a formal meta-analysis as an important application of, and to draw on caveats associated with, latitudinal gradients. Finally, we look forward to approaches to deal with these complexities to achieve robust inference about warming impacts on terrestrial organisms.

Patterns of environmental variation across latitudes

TEMPERATURE

As a general rule, temperature as well as growing season length decrease towards the poles. The slope of the

relationship between latitude and mean annual temperatures (MAT) is $-0.73\text{ }^{\circ}\text{C}$ per degree of latitude in the Northern extratropical hemisphere (Fig. 1a,b), equivalent to $154\text{ km }^{\circ}\text{C}^{-1}$ (i.e. a 154 km northwards shift is needed for MAT to drop $1\text{ }^{\circ}\text{C}$). When considering only the mean growing season (March–September) or the warmest month (July), the temperature gradient amounts to only $-0.65\text{ }^{\circ}\text{C}$ per degree of latitude ($171\text{ km }^{\circ}\text{C}^{-1}$) and $-0.48\text{ }^{\circ}\text{C}$ per degree of latitude ($231\text{ km }^{\circ}\text{C}^{-1}$), respectively (Fig. 1b). The mean latitudinal temperature gradient thus decreases in the period when most terrestrial organisms are active, meaning that the northward shift required for temperatures to drop $1\text{ }^{\circ}\text{C}$ increases. Moreover, there is a poleward decline in growing season length, and an increase in the amount of temperature seasonality, interannual variability and strength of winter frost (Pau *et al.* 2011). Winter can be extremely harsh and prolonged closer to the poles, and the amount of snow and clouds generally increases with latitude (Woodward 1987). Finally, the latitudinal MAT gradient is lower in the Southern extratropical hemisphere ($-0.57\text{ }^{\circ}\text{C}$ per degree of latitude), but steeper in North America ($-0.77\text{ }^{\circ}\text{C}$ per degree of latitude) than in Eurasia ($-0.69\text{ }^{\circ}\text{C}$ per degree of latitude), indicating that MAT changes faster with latitude in North America (cf. Rejmánek 2000; Petitpierre *et al.* 2012).

These latitudinal clines mask a large variability in temperature due to local factors: vegetation type and structure, topography, wind speed, radiation balance, cloud and snow cover and atmospheric moisture will all affect the local temperature experienced by terrestrial organisms (Woodward 1987; Körner 2003, 2007; Scherrer & Körner 2010; Scherrer, Schmid & Körner 2011; Graae *et al.* 2012). Extensive snow cover, for instance, creates a thermally isolating layer in high-latitude ecosystems (Bartlett, Chapman & Harris 2004) affecting the phenology, survival and growth of short plants (Bokhorst *et al.* 2011). Together, these factors can significantly alter

temperatures at smaller spatial scales. In a latitudinal comparison of temperatures measured at the soil surface in forest understories with air temperatures measured at nearby weather stations, Graae *et al.* (2012) showed that the microclimatic decoupling can amount to $2\text{--}8\text{ }^{\circ}\text{C}$ due to factors such as shading, snow cover and evapotranspiration. Even more, a remarkably constant tree leaf temperature of *c.* $21\text{ }^{\circ}\text{C}$ between latitudes of 18°N and 68°N has recently been found (Helliker & Richter 2008). Hence, while there is a clear macroclimatic gradient across latitudes, microclimatic variation requires measuring temperatures also in the actual study sites, for example using data loggers or thermal imagery (Scherrer & Körner 2010; Scherrer, Schmid & Körner 2011; Graae *et al.* 2012).

PRECIPITATION

The amount and seasonality of precipitation is also a major determinant of the distribution of vegetation types across the world (Whittaker 1975). The latitudinal slope coefficient in mean annual precipitation amounts to -4.04 mm per degree of latitude in the Northern extratropical hemisphere, but many regions deviate from this mean pattern due to the proximity of oceans, mountains and major wind flows (Fig. 2a). Conversely to temperature, the interannual variability and seasonality in precipitation tends to decrease towards the pole in the Northern hemisphere (Pau *et al.* 2011). Nevertheless, latitudinal precipitation gradients can be used to infer potential responses to, for instance, drought events (e.g. Ramírez-Valiente *et al.* 2009).

PHOTOPERIOD, LIGHT QUALITY AND QUANTITY

The daily and seasonal light cycle is a very important environmental factor for organisms because photoperiod and light levels greatly influence biological activity (Hay 1990; Mills

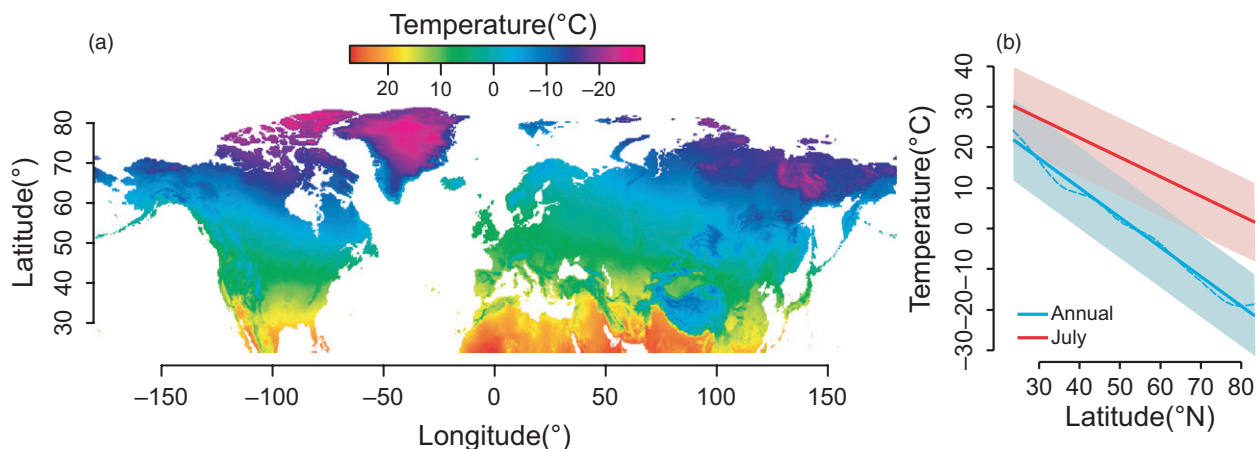


Fig. 1. The latitudinal temperature gradient in the Northern extratropical hemisphere. (a) Map of the mean annual temperature in the Northern extratropical hemisphere. (b) Relationships between latitude and mean annual and July temperatures. The mean latitudinal temperature gradient decreases in the period when most terrestrial organisms are active in the Northern hemisphere. Solid lines represent linear regressions ($R^2 = 0.825$ and 0.692 for annual and July temperatures, respectively), the dashed blue line a general additive model of the annual temperature (adj. $R^2 = 0.829$). Shaded areas represent the 95% prediction intervals. All relationships are highly significant ($P < 0.0001$ and $n = 385\,904$ grid cells; WorldClim data, Hijmans *et al.* 2005).

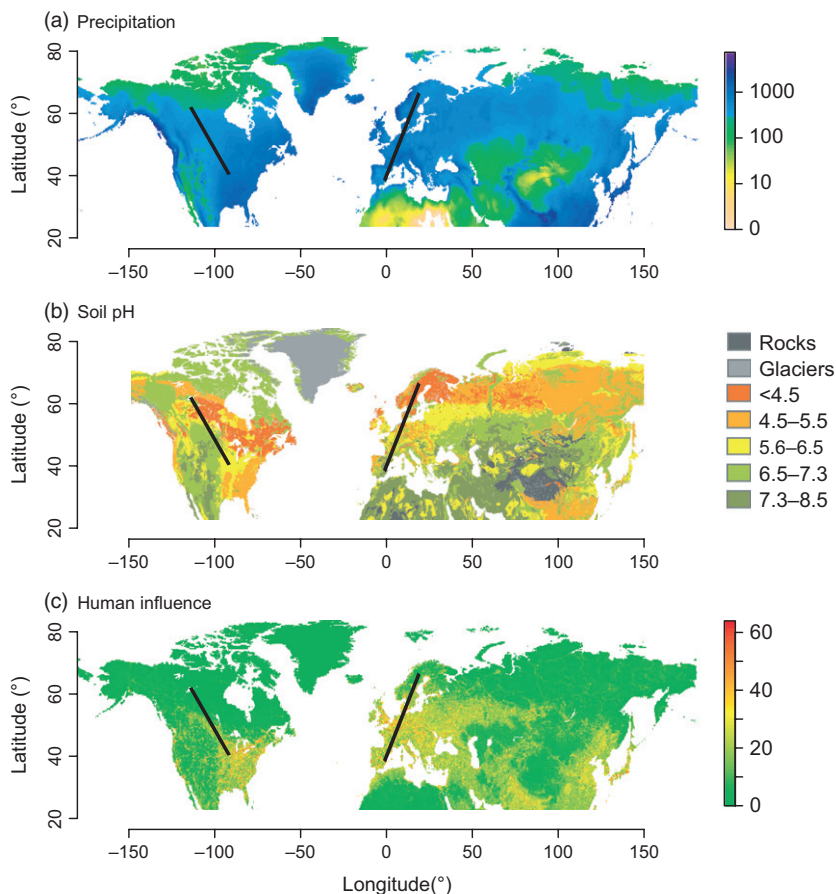


Fig. 2. Variation in (a) mean annual precipitation (mm), (b) soil pH and (c) the human influence index in the Northern extratropical hemisphere. The black lines depict two hypothetical examples of temperature gradients showing covariation with precipitation, soil pH and human influence. (a) Precipitation data from WorldClim, Hijmans *et al.* (2005). Note the log-transformed scale to better see the differentiation between high versus low-precipitation areas. (b) Soil pH–H₂O data from Batjes (2012). (c) Human influence index from Last of the Wild Data Version 2 (2005). This index was calculated by integrating information on human settlement (population density, built-up areas), access (roads, railroads, navigable rivers and coastline), landscape transformation (land use) and electric power infrastructure (night-time lights), and ranges from 0, that is, no human influence, to 64, that is, high human influence (Sanderson *et al.* 2002).

2008; Jackson 2009; Saikkonen *et al.* 2012). In the summer, daylight amounts to 24 h per day north and south of the Arctic and Antarctic Circle (at 66° 33' latitude), respectively. As the seasonality of photoperiod increases with latitude, so does its biological relevance. Also the seasonal variation in the distribution of semi-darkness such as twilight and moonlight increases towards the poles affecting the phenology and behaviour of organisms (Mills 2008). Furthermore, the amount of solar ultraviolet radiation decreases towards higher latitudes due to greater prevailing solar angles and atmospheric ozone concentration (Caldwell 1981), while the duration of enhanced far-red to red ratios at the beginning and end of each day are considerably longer at higher latitudes (Hay 1990). Thus, various aspects of light (quality and quantity) differ strongly across latitudes.

SOIL CHARACTERISTICS AND NUTRIENT AVAILABILITY

Soil characteristics and nutrient availability are important determinants of the productivity and community composition of terrestrial ecosystems. In the Northern extratropical hemisphere, there is a general poleward decrease in soil pH (Pärtel 2002; Fig. 2b) and decomposition and mineralization rates (Berg *et al.* 1993; Gholz *et al.* 2000; but see Giardina & Ryan 2000), while soil organic carbon concentration tends to increase (e.g. Jones *et al.* 2004). Whereas soil phosphorus (P) availability may limit plant growth near the equator, soil

nitrogen (N) tends to be limiting at higher latitudes (Reich & Oleksyn 2004; Lovelock *et al.* 2007; Sardans, Rivas-Ubach & Peñuelas 2012). However, the decades-long enhanced deposition of reactive N in industrialized regions may have altered these conditions (Bobbink *et al.* 2010; Peñuelas *et al.* 2012). Depending on the study scale, the input of eutrophying and acidifying reactive N can covary with latitude. For instance, there are strong gradients in wet and dry total nitrogen deposition rates (NH_x and NO_y) from the central US towards northern Canada, from central towards northern Europe as well as from central China towards Siberia (Bobbink *et al.* 2010). In addition, rising temperatures have often been shown to accelerate N cycling in ecosystems (Peterjohn *et al.* 1994; Rustad *et al.* 2001).

BIOTIC INTERACTIONS

The widespread decrease in biodiversity from the tropics towards the poles is consistent across many taxa, habitats, and spatial and temporal scales (Fischer 1960; Huston 1994; Hillebrand 2004). Various mechanisms have been proposed to explain this latitudinal decline in diversity, including stochastic processes, the mid-domain effect, and variation in evolutionary rates, as well as decreasing energy supply, biome area and range sizes (Gaston 2000; Willig, Kaufman & Stevens 2003; Hillebrand 2004). In addition, the intensity of biotic interactions may vary with latitude. It has been

argued that biotic interactions such as those between plants and their herbivores, pathogens or mutualistic fungi are less prevalent at higher latitudes (reviewed by Schemske *et al.* 2009). Defence mechanisms such as spines and enhanced alkaloid concentrations to resist herbivory have been shown to be more common in low-latitude plants than in high-latitude plants (Levin 1976; Pennings, Siska & Bertness 2001; Rasmann & Agrawal 2011). However, evidence to the contrary is increasing recently (Adams & Zhang 2009; Moles *et al.* 2011a,b). Moles *et al.* (2011b), for instance, attributed enhanced defence for plants at higher latitudes to the increased costs of losing leaf tissue in harsh environments. Furthermore, endophytic fungi infection incidence, which can provide protection against pathogens, has been shown to decrease from tropical over temperate to Arctic plants (Arnold & Lutzoni 2007; Schemske *et al.* 2009). There is only scarce information available on the global distribution patterns of microscopic below-ground organisms, in spite of their importance for carbon and nutrient cycling and their contribution to global biodiversity (Decaëns 2010). For example, species richness of mycorrhizal fungi does not seem to follow the general latitudinal diversity gradient (Brundrett 2009; Öpik *et al.* 2010).

HUMAN INFLUENCE

Human population densities and influence on ecosystems also vary with latitude. For instance, the Human Influence Index, a proxy for human influence on terrestrial ecosystems using information on human settlement, access, land use and electric power infrastructure (Sanderson *et al.* 2002; Last of the Wild Data Version 2 2005) decreases from central to northern Europe and North America and from southeast Asia to northern Siberia (Fig. 2c). Human influence, of which habitat fragmentation, loss and deterioration are probably most important, affect the population dynamics and abundance of numerous species as well as patterns of biodiversity (Fahrig 2003). Importantly, the negative effects of habitat fragmentation are greatest in areas with higher maximum temperatures (Mantyka-Pringle, Martin & Rhodes 2012) and exacerbate the effects of climate change in general as habitat fragmentation impedes distribution range shifts (Davis & Shaw 2001; Hof *et al.* 2011).

Latitudinal intraspecific variation in plant traits: a meta-analysis

Latitudinal environmental variation (cf. previous section) is associated with large intraspecific trait differences, whose importance for population and community dynamics is increasingly being recognized (Violle *et al.* 2012). Therefore, a meta-analysis on intraspecific latitudinal trait variation is timely and needed. Assessing intraspecific trait variation by comparing populations of the same species growing in different climates is a particularly valuable approach to address the effects of climate change on terrestrial organisms (see e.g. Daws *et al.* 2004; Reich & Oleksyn 2008; De Frenne *et al.*

2009, 2011a; Ramírez-Valiente *et al.* 2009; Qiu *et al.* 2010). Here, we perform a meta-analysis of the latitudinal intraspecific variation in five key functional traits related to the reproduction, growth, function and survival of plants, namely plant height, specific leaf area (SLA), leaf nitrogen:phosphorus (N:P) stoichiometry, seed mass and root:shoot (R:S) ratio. Plant height and seed mass are key ecological traits as they control access to light, escape from predators and disturbance, dispersal distances, soil seed bank persistence, germination potential, seedling establishment, and community assembly (Westoby 1998; Ehrlén & Eriksson 2000; Coomes & Grubb 2003; Moles *et al.* 2007, 2009). The SLA (leaf area divided by its dry weight) is related to the growth rate and ecological strategy of plants (Westoby 1998; Poorter *et al.* 2009). The balances of available N and P, on the one hand, and above-ground and below-ground biomass, on the other hand, affect many processes in terrestrial ecosystems such as decomposition of litter, biotic interactions and adaptation to stress (Güsewell 2004; Sardans, Rivas-Ubach & Peñuelas 2012). Within species, the variation in these life-history traits is determined by factors such as temperature, water availability, light and nutrient supply, CO₂ concentration and defoliation (Wilson 1988; Coomes & Grubb 2000; Poorter *et al.* 2009) and is thus expected to strongly vary across latitudes.

DATA COLLECTION AND ANALYSES

We searched the scientific literature for studies comparing plant individuals from at least two distinct latitudinal populations (more than one latitudinal degree apart) of the same species, either in natural populations or grown in common gardens (i.e. individuals sampled in different sites along a latitudinal gradient and then transplanted and measured in a common garden). We identified 73 published articles dealing with 98 species and resulting in 155 species × trait combinations (see Appendix S1 in Supporting Information for a full reference list and supplementary methods). The mean number of populations investigated per species was 28.6 (median 14, range 2–424), while the mean latitudinal range was 13.8° (median 11.0°, range 1.1–47.0°). Of the species included, 49% were herbs, 29% trees, 14% graminoids and 8% shrubs (Appendix S1). We first classified each study on the basis of the patterns found with latitude (statistically significantly increasing trait value towards the poles, decreasing, or non-significant) and temperature (statistically significantly increasing trait value with temperature, decreasing, or non-significant). Second, we extracted the slope coefficient of the regression between each of the traits and the latitude, relatively expressed in percentage change per degree of latitude (slope coefficient available for 88 species, giving 137 species × trait combinations). The mean slope for each trait as well as the standard deviation and confidence intervals of the slopes were calculated by bootstrapping 999 times with each slope weighted by the number of populations times the latitudinal range from that study (in other words, studies with many sampled populations and a wide latitudinal range contributed more to the overall mean) using

the *boot*-function of the *boot*-library in R 2.15.1 (R Development Core Team 2012; see Appendix S1 for more information). Finally, for those species where a latitudinal slope was available from natural populations and a common garden (nine species, 15 species \times trait combinations), we divided the latitudinal slope in the common gardens by the slope in the natural populations (comparable with a response ratio in standard meta-analyses) and followed the same bootstrapping technique for calculating the mean ratio and confidence interval.

RESULTS AND DISCUSSION

We found large variation in the trait responses to 'latitude'. Across all species and considering both natural populations and common gardens, leaf N:P ratio and seed mass were significantly lower in high-latitude than in low-latitude populations; the slope coefficients were negative and significantly different from zero (Fig. 3a). However, half of the identified

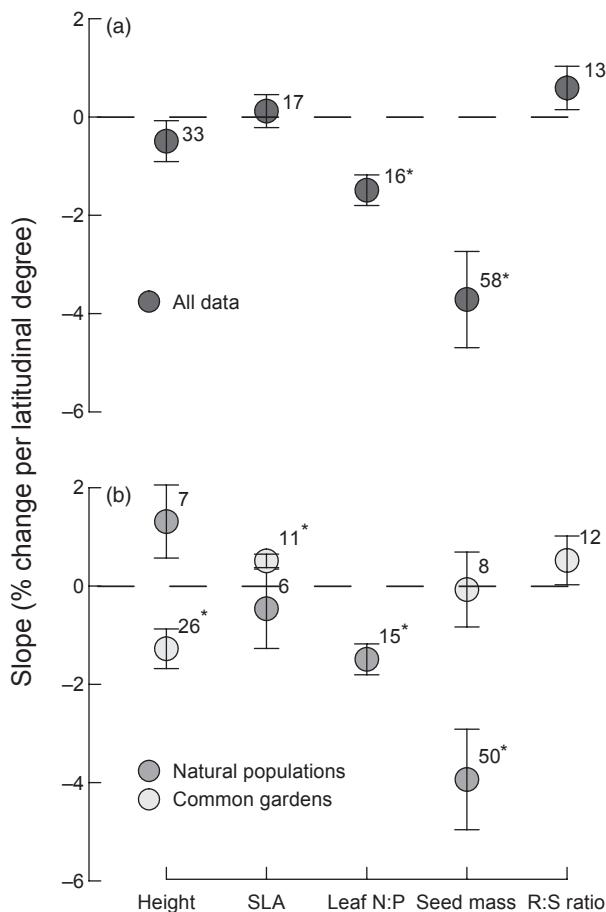


Fig. 3. Slope coefficients (mean \pm SD) of the intraspecific life-history trait variation with latitude (a) for all data, and (b) in plants sampled in natural populations and in common gardens. A negative slope coefficient indicates higher trait values in low-latitude than in high-latitude populations, and vice versa. The numbers refer to the number of species; traits with less than five replicate species were omitted from the analyses in (b). * $P < 0.05$. SLA, specific leaf area; N : P, ratio of leaf nitrogen/phosphorus concentrations; R : S, ratio of below-ground/above-ground dry biomass.

studies that reported on intraspecific plant trait variation have been performed in natural populations (52%) and the other half in common garden experiments (48%; Appendix S1). Natural populations and common garden experiments should be considered separately because common gardens mainly reflect adaptive differentiation, whereas natural conditions reveal natural selection as well as plastic responses to the environment. Significant discrepancies emerge between the outcomes of both approaches (Fig. 3b). The latitudinal decline in leaf N:P ratio and seed mass is mainly driven by the patterns found in natural populations. Conversely, the plant height decreased and SLA increased significantly with the latitude of population origin in common garden experiments, but not in field studies (Fig. 3b). For species where data from both natural populations and common gardens are available, results are generally consistent; the mean ratio of the latitudinal slope in the common gardens and natural populations was 0.140 (± 0.757 SD, 95% confidence interval $-1.26, 1.62$; i.e. including one). The finding of consistent trait variation between provenances in the field and in common gardens stresses – at least within these study species – the importance of directional selection and adaptation to local environmental factors (Kawecki & Ebert 2004; Leimu & Fischer 2008; Montesinos-Navarro *et al.* 2011) which might affect the ability of these plant populations to respond to future climate change (Reed, Schindler & Waples 2011; Bennington *et al.* 2012).

As with the interspecific latitudinal gradients in plant height (Moles *et al.* 2009), seed mass (Moles *et al.* 2007) and leaf N:P (Reich & Oleksyn 2004), the latitudinal clines within species also appear to be significant (for seed mass variation within species, see also Moles & Westoby 2003). The mean slope for plant height (common gardens) and seed mass (natural populations) amounted to -1.28% and -3.94% per latitudinal degree, respectively. Thus, plants of the same species from low-latitude populations grow on average *c.* 1.3% taller in common gardens and produce *c.* 4% heavier seeds in the field per latitudinal degree than plants from high-latitude populations. The magnitude of the slope coefficient for seed mass is comparable with the intraspecific slope coefficient calculated by Moles & Westoby (2003) who reported a 1.9-fold reduction in seed mass per 20° of latitude. A negative intraspecific latitudinal slope coefficient is probably related to (i) shorter growing seasons that reduce the time for plant growth and seed development, (ii) lower mean temperatures that decrease net primary productivity at higher latitudes (Baker 1972; Moles & Westoby 2003; Moles *et al.* 2007), (iii) shifts in mating system (Darling, Samis & Eckert 2008), (iv) trade-offs between seed mass and frost tolerance (Agrawal, Conner & Stinchcombe 2004) or (v) may arise from the effects of post-glacial migration (Cwynar & Macdonald 1987). Yet, the latitudinal relationships show large variation within the different studies (Fig. 4a). For instance, *Milium effusum*, a European understory forest grass, grows taller in natural populations in the north probably due to increased northerly light availability and canopy openness (De Frenne *et al.* 2011b). Similarly, *Verbascum thapsus* plants from mid-latitudes

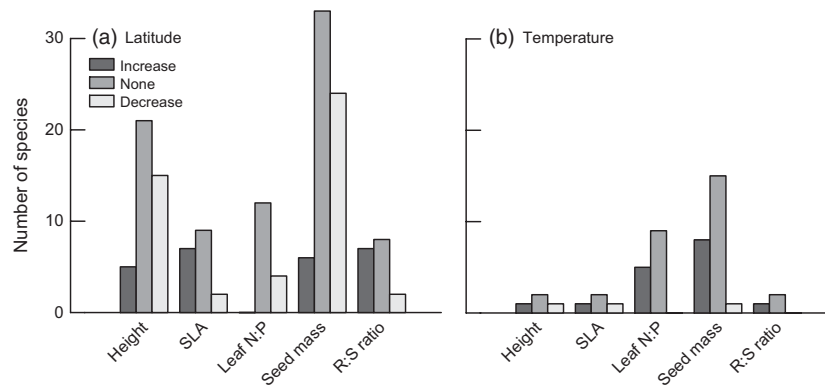


Fig. 4. Quantification of the intraspecific latitudinal life-history trait variation identified in 98 plant species (155 species \times trait combinations) as the number of species displaying statistically significant trait variation with (a) latitude and (b) temperature. Less than a third of the latitudinal transect studies included in our synthesis specifically assessed the effects of temperature. *Increase/Decrease*: trait value increases/decreases statistically significantly with latitude of origin or with temperature; *None*: non-significant linear latitudinal or temperature pattern, or significant differences among populations but not directly related to latitude or temperature.

(North Carolina, USA) were smaller than more southern (Texas, USA) and northern (Canada) ecotypes where competition is less intense (Reinartz 1984).

Foliar N:P ratios were also found to significantly decrease towards the poles in natural populations (Fig. 3). This can largely be explained by direct temperature effects on plant biochemistry and physiology and by limitation of soil P in the tropics and of soil N at higher latitudes (McGroddy, Daufresne & Hedin 2004; Reich & Oleksyn 2004; Lovelock *et al.* 2007). Similar latitudinal clines in N:P ratios have also been found in senesced litter (Yuan & Chen 2009), fine roots (Yuan, Chen & Reich 2011) and seeds (De Frenne *et al.* 2011c). The higher SLA in high-latitude than in low-latitude plants in common garden experiments might reflect adaptive differentiation to latitudinal changes in temperature, precipitation and light availability, all of which have important effects on SLA (Poorter *et al.* 2009). Finally, the slope coefficient of root:shoot ratio changes with latitude was not significantly different from zero. Although some studies have reported higher investment in below-ground organs and enhanced clonal reproduction in high-latitude populations (Billings & Mooney 1968; Dorken & Eckert 2001; Crawford 2008), this trait may be more influenced by local environmental variables without a clear latitudinal pattern (e.g. disturbance and stress).

Importantly, less than a third of the latitudinal transect studies included in our synthesis specifically assessed the effects of temperature (31.6%) or some other environmental factor such as precipitation and soil characteristics (3.9%) on plant traits. The remainder (64.5%) only evaluated the presence of latitudinal patterns on plant traits, that is, mainly using *latitude* as the only explanatory variable. Hence, albeit of course valuable for other questions, few studies specifically attempt to disentangle temperature from other latitudinal factors (Fig. 4a vs. Fig. 4b), which prevents further analyses about the strength of trait change with temperature. These results illustrate that latitudinal gradients are still an underutilized resource for ecological climate change research. The next section deals with this issue.

Looking forward: using latitudinal gradients to infer warming effects

Many species' characteristics vary with latitude (cf. meta-analysis section) and the temperature variation found across latitudes (cf. review section) thus offers an excellent opportunity to unravel the relative importance of temperature on organisms. However, inferences of likely temperature effects along latitudinal gradients are in many cases inadequate (Fig. 4a vs. 4b), very often due to different study aims and experimental design, and/or limited data analyses in the context of climate warming. As a result, latitudinal gradients are a currently underutilized resource in a climate change context. Here, we link aspects from the review and meta-analysis sections, raise awareness of these problems and suggest possible ways of overcoming them. First, data collection and analysis should carefully deal with the fact that many environmental variables other than temperature also vary with latitude. Thus, to ascertain the role of temperature on biological traits and processes, latitudinal patterns in biological characteristics should be evaluated against temperature and covarying environmental variables instead of using *latitude* as a 'surrogate' (Körner 2007). Second, experimental data or auxiliary information may be required to determine how much of the observed phenotypic differences across latitudes are due to plastic responses versus adaptive differentiation between populations.

COVARIATION OF ENVIRONMENTAL FACTORS WITH TEMPERATURE

Given the concurrent variation of multiple environmental factors across latitudes, disentangling temperature effects can be complicated (cf. Körner 2007; Bradshaw & Holzapfel 2008, 2010). While this limitation is shared with other gradient analyses such as altitudinal transects (Fukami & Wardle 2005; Körner 2007; Nogués-Bravo *et al.* 2008), the patterns of variation of the 'confounding' factors will be different

across latitudes, stressing the need for complementary approaches. For instance, photoperiod is likely one of the most difficult abiotic factors to unravel from temperature effects when working along latitudinal gradients (Bradshaw & Holzapfel 2008, 2010; De Frenne *et al.* 2011a,b), whereas this does not represent a problem in most altitudinal gradient studies that span a small latitudinal range. Likewise, precipitation and temperature have different patterns of covariation across altitudinal and latitudinal gradients (e.g. as demonstrated by McCain & Colwell 2011) or may be roughly orthogonal (e.g. in the Midwestern USA; Figs 1 and 2a), which could be harnessed to disentangle the effects of both variables by integrating data from multiple approaches.

Several general recommendations can be put forward to overcome the problem of covarying environmental factors. First, whenever possible, study sites could be carefully selected so as to minimize the covariation between temperature and potential confounding factors, for example by working within similar precipitation regimes or soil types (Körner 2007; De Frenne *et al.* 2009). Second, replication across space and time will greatly help to disentangle the effects of the different environmental factors (e.g. Sugiyama 2003; Ibáñez *et al.* 2007; Ramírez-Valiente *et al.* 2009; De Frenne *et al.* 2010). Spatiotemporal replication may permit researchers to separate the effects of temperature while controlling for factors with different frequency or scale of variation (e.g. soil properties, precipitation, human influence, and photoperiod). For instance, De Frenne *et al.* (2010) found consistently positive temperature effects on the sexual reproduction of the forest understory herb *Anemone nemorosa* during 3 years of seed sampling in populations located in similar forests, precipitation regimes and soil types along a latitudinal gradient in NW-Europe. Third, appropriate statistical techniques such as multiple regression, hierarchical or mixed-effect models, variation partitioning, or structural equation modelling (e.g. De Frenne *et al.* 2009; Milla, Escudero & Iriondo 2009; Stomp *et al.* 2011) should be used to statistically control for confounding factors. For example, structural equation models were applied along latitudinal gradients to determine the causal relationships between seed origin and several plant traits and fitness of the annual *Lupinus angustifolius* (Milla, Escudero & Iriondo 2009), and between phytoplankton species richness and environmental variation in US freshwater lakes (Stomp *et al.* 2011). Hence, univariate analyses using *latitude* as the single factor are insufficient to move from detecting a 'latitudinal effect' to properly inferring species' responses to temperature.

PLASTIC RESPONSES VERSUS ADAPTIVE DIFFERENTIATION

A second key question in the interpretation of latitudinal gradient studies is how much of the observed patterns are due to plastic responses or due to adaptive differentiation between populations. Genetic differentiation between populations is common (e.g. Petit *et al.* 2005), and many populations show local adaptation to their *home* environment (Leimu & Fischer

2008). Also, the process of post-glacial recolonization in the Northern hemisphere has generated a latitudinal pattern of genetic differentiation, with northernmost populations usually showing reduced neutral genetic diversity (Hewitt 2000; Davis & Shaw 2001). If phenotypic differences across latitudes are driven by genetic differentiation, any association with temperature will be ambiguous. Powerful approaches to ascertain plastic versus adaptive effects on phenotypes are the combination of natural populations with common garden and transplant experiments (e.g. Clausen, Keck & Hiesey 1940; De Frenne *et al.* 2011a; Montesinos-Navarro *et al.* 2011; Shaw & Etterson 2012; Woods *et al.* 2012). In such experiments, specimens are grown in a common environment or transplanted to different regions. These set-ups thus allow the determination of the adaptive basis of life-history trait variation. Hence, an integrated approach combining data from natural populations and common gardens is critical to unravel adaptive clines (e.g. Shaw & Etterson 2012; Woods *et al.* 2012).

INTEGRATION OF METHODS: THE WAY FORWARD

For all these reasons, the integrated use of latitudinal, altitudinal, and temporal temperature gradients, common garden experiments and experimental warming studies represents a promising way forward in the quest for better understanding and forecasting the potential implications of global warming on plant populations and communities (Shaver *et al.* 2000; Dunne *et al.* 2004; Fukami & Wardle 2005; Rustad 2008). Integrated methods are increasingly being advocated (Harte & Kueppers 2012; Kawecki *et al.* 2012; Shaw & Etterson 2012). Integration allows researchers (i) to overcome the drawbacks of the individual methods, (ii) to resolve the adaptive basis of geographic variation by, for example, using a combination of temperature gradients and common garden experiments (Shaw & Etterson 2012), (iii) the covariation of temperature with other environmental variables is probably different for each technique, (iv) spatiotemporal scales vary greatly among them and (v) experiments may provide a mechanistic understanding of patterns observed in observational studies. For instance, the plant height of the forest understory geophyte *Anemone nemorosa* increased with temperature, both in open-top chambers as well as in response to southward transplantation along a latitudinal gradient (De Frenne *et al.* 2011a), which suggests that this might also occur in response to future climate warming. Similarly, Dunne, Harte & Taylor (2003) and Dunne *et al.* (2004) showed that earlier snowmelt dates in subalpine meadows advanced flowering of *Delphinium nuttallianum*, regardless of how this was assessed: along elevational gradients, by comparing inter-annual differences or by using infrared heaters. On the other hand, in the case of the grass *Dactylis glomerata*, Sugiyama (2003) described a hump-shaped temperature – seed mass relationship along a latitudinal gradient in Japan, while Dainese (2011) reported significant positive effects of temperature across elevations in the Alps. Another valuable approach can be to sample individuals along a climatic gradient and grow

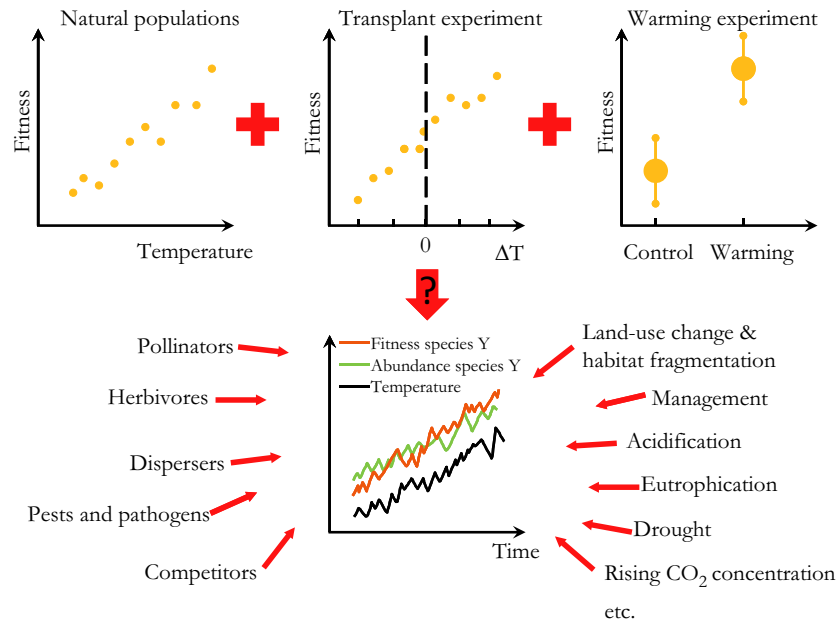


Fig. 5. An integrated quantification of fitness responses in natural populations and common garden transplant experiments along temperature gradients, and in warming experiments, contribute to a better understanding of the potential species and community responses to temperature changes. For instance, if the fitness of species Y increases with temperature in natural populations, decreases in response to poleward/upward translocation along a latitudinal/altitudinal gradient, and increases in response to experimental warming, this is a clear indication that warming might also result in enhanced fitness for this species over time. Subsequently, the abundance of species Y might increase, depending on the simultaneous response of co-occurring competitors, pollinating and dispersing agents, herbivores and pests, interaction with other global-change drivers, etc., all of which increase the uncertainty on the demography of species Y and the population and community-level responses. ΔT : difference in temperature between site of origin and site of the common garden or transplant experiment.

the resulting material in growth chambers in which the factor of interest can be experimentally controlled. For instance, Souther, Lechowicz & McGraw (2012) transplanted contrasting *Panax quinquefolius* provenances into growth chambers with different temperatures but did not find a *home temperature* benefit as expected if individuals were only locally adapted to temperature. The identification of comparable or contrasting responses in different observational and experimental settings allows researchers to distinguish between consistent and dynamic or context-dependent responses to climate warming (Dunne *et al.* 2004) and to further our mechanistic understanding of the role of temperature on ecosystem processes. Such an integrated combination will likely improve predictions on trait responses, changes in fitness of individuals, distributions of populations and community composition (Harte & Kueppers 2012; conceptually summarized in Fig. 5).

Conclusions

The variation in ecosystem structure and composition between the tropics and the poles has enthused ecologists for a long time. Latitudinal gradients provide an exciting natural laboratory for ecological research to better understand potential impacts of changing temperatures on terrestrial organisms. In natural populations, we found leaf N:P ratios and seed mass to be significantly lower in high-latitude than in low-latitude populations. On the other hand, the plant height decreased and SLA increased significantly with latitude of population origin in common garden experiments indicating adaptive

differentiation across latitudes. Moving on from these latitudinal effects to clearly inferring a temperature signal appears as an important step. Therefore, confounding environmental factors other than temperature and adaptive versus plastic responses need careful consideration. Latitudinal gradients are still an underutilized resource in this respect. More generally, the integration of evidences obtained from a variety of studies emerges as the way forward to increase our knowledge about the potential implications of climate warming on species in the coming decades.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods and reference list for the literature review.