

# Plant movements and climate warming: intraspecific variation in growth responses to nonlocal soils

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## Summary

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Received: 16 October 2013

Accepted: 30 November 2013

*New Phytologist* (2014) **202**: 431–441  
doi: 10.1111/nph.12672

**Key words:** climate change, climate envelope, common garden experiment, forest understorey, intraspecific variation, *Milium effusum* (millet grass), range shifts, soil biota.

- Most range shift predictions focus on the dispersal phase of the colonization process. Because moving populations experience increasingly dissimilar nonclimatic environmental conditions as they track climate warming, it is also critical to test how individuals originating from contrasting thermal environments can establish in nonlocal sites.
- We assess the intraspecific variation in growth responses to nonlocal soils by planting a widespread grass of deciduous forests (*Milium effusum*) into an experimental common garden using combinations of seeds and soil sampled in 22 sites across its distributional range, and reflecting movement scenarios of up to 1600 km. Furthermore, to determine temperature and forest-structural effects, the plants and soils were experimentally warmed and shaded.
- We found significantly positive effects of the difference between the temperature of the sites of seed and soil collection on growth and seedling emergence rates. Migrant plants might thus encounter increasingly favourable soil conditions while tracking the isotherms towards currently 'colder' soils. These effects persisted under experimental warming. Rising temperatures and light availability generally enhanced plant performance.
- Our results suggest that abiotic and biotic soil characteristics can shape climate change-driven plant movements by affecting growth of nonlocal migrants, a mechanism which should be integrated into predictions of future range shifts.

## Introduction

The global climate is changing several orders of magnitude faster than in the past 65 million yr (Diffenbaugh & Field, 2013). Changing climatic conditions are affecting the fitness of many species and ecosystems, and are forcing numerous species to migrate towards higher elevations or latitudes to maintain their distribution within thermal limits (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Peñuelas *et al.*, 2013). A recent meta-analysis showed that species' ranges are shifting at median rates of  $1.1 \text{ m yr}^{-1}$  elevation and  $1.7 \text{ km yr}^{-1}$  latitude across birds, mammals, arthropods, molluscs, amphibians, reptiles, fish, algae and plants (Chen *et al.*, 2011), but individual species vary greatly in their estimated migration rates (Parolo & Rossi, 2008; Berg *et al.*, 2010; Chen *et al.*, 2011; Svenning & Sandel, 2013).

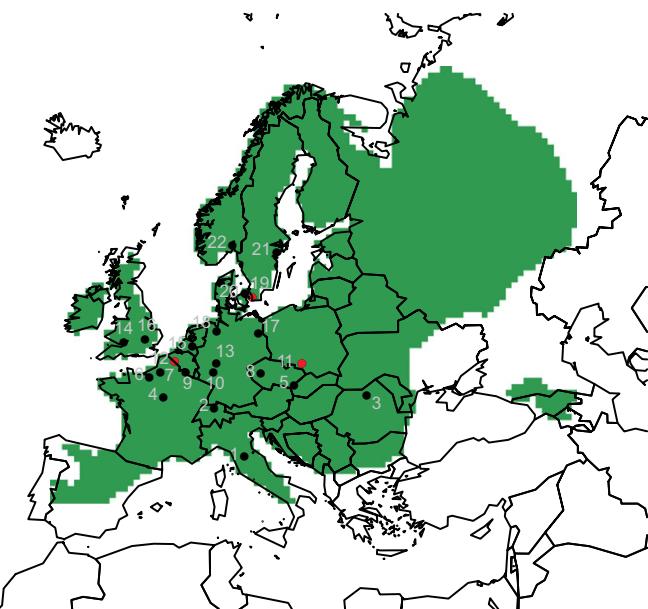
Intraspecifically, it is expected that climate warming will differentially affect populations across the distribution range of species (Reich & Oleksyn, 2008; De Frenne *et al.*, 2011a). Yet, knowledge about intraspecific spatial reordering in response to climate change is scarce (Pauls *et al.*, 2013). Even less is known about the future performance of migrants in their new habitats (Engelkes *et al.*, 2008; Ibanez *et al.*, 2009; van Grunsven *et al.*, 2010). To reliably forecast species responses to the projected climate shifts, it is therefore of crucial importance not only to evaluate the extent to which populations might be able to disperse through the landscape (Corlett & Westcott, 2013), but also to test how populations originating from different thermal environments can establish and perform in nonlocal sites after dispersal (van der Putten *et al.*, 2010).

Within individual species, dispersal and natural selection generally result in populations that are adapted to the local environment (Kawecki & Ebert, 2004). Local adaptation has been detected across a wide range of spatial scales. Temperature and precipitation are key agents of natural selection that may lead to local adaptation in plants at larger scales (Linhart & Grant, 1996; Joshi *et al.*, 2001; Macel *et al.*, 2007; De Frenne *et al.*, 2011a; Ågren & Schemske, 2012). At smaller spatial scales, abiotic soil characteristics such as nutrient availability and soil texture, but also biotic soil factors including below-ground interactions (e.g. those with root-feeding nematodes, mycorrhizal fungi or co-occurring plant species), can lead to local adaptation (Macel *et al.*, 2007; Grondahl & Ehlers, 2008; Sherrard & Maherli, 2012; Smith *et al.*, 2012). Local adaptation generally results in improved fitness of each population under its own local environmental conditions (Leimu & Fischer, 2008) and is thus of fundamental importance to the potential movement of plants in response to climate warming: individuals tracking the shifting isotherms might be maladapted to nonclimatic factors such as abiotic and biotic soil characteristics in nonlocal sites (Corlett & Westcott, 2013). As moving populations will probably experience increasingly dissimilar nonclimatic environmental conditions, lack of adaptation to nonlocal soils could result in fitness losses. On the other hand, the release from local natural enemies, such as soil pathogens and below-ground herbivores, might enhance plant performance (van Grunsven *et al.*, 2010). Natural enemy release is one of the key reasons for the success of invasive

plant species in colonizing novel habitats (Reinhart *et al.*, 2003; Callaway *et al.*, 2004; Wolfe & Klironomos, 2005), but the impact of soil biota might also be important for climate change-driven plant movements (van Grunsven *et al.*, 2007, 2010; Engelkes *et al.*, 2008; Berg *et al.*, 2010; van der Putten *et al.*, 2010).

Here, we assess the intraspecific variation in plant responses to nonlocal soils by planting a widespread Holarctic grass of deciduous forests, *Milium effusum*, into an experimental common garden using seeds and soil sampled in 22 sites across a large part of its European distributional range (Fig. 1). The various combinations of seeds and soils (e.g. southern individuals planted into northern soils) correspond to virtual movement scenarios of up to 1600 km, and thus reflect possible soils that plants might experience while tracking climate warming. We quantified seedling emergence and performance of the resulting plants subjected to two possible future temperature scenarios. In addition, light conditions were experimentally manipulated to simulate forest canopy openings vs shade, as tree canopy cover in *M. effusum* populations in European deciduous forests tends to decrease towards the north (De Frenne *et al.*, 2011b). Changes in forest canopy cover might thus influence growth of migrant populations separately from macroscale temperature and soil effects.

Using *M. effusum* as our study species, we assessed establishment of migrant populations in the face of climate warming. We specifically addressed whether the temperature difference between the sites of seed and soil collection, experimental warming and shading, and their interactions, affected seedling emergence and plant growth across the distribution of the species in northwest Europe. Additionally, the plant responses and the temperature differences between the sites of seed and soil collection were related to changes in other environmental variables (e.g. soil



**Fig. 1** Sites where seeds and soils were collected. The red circles denote the *Milium effusum* populations that were used as migrant populations (and thus sown in nonlocal soils, i.e. northern Belgium, southern Poland, southern Sweden). The green area depicts the current distribution range of *M. effusum* in Europe (Lambert Azimuthal Equal Area projection, after Hultén & Fries, 1986). Numbers refer to site descriptions in Table S1.

characteristics, nitrogen deposition, precipitation) between the sites from which seeds and soils were collected to explain the emerging patterns.

## Materials and Methods

### Study species

*Milium effusum* L. (Poaceae) is a hemicryptophytic, early-summer flowering grass distributed across large parts of Europe (Fig. 1), primarily occurring in deciduous forests. It is a characteristic species of beech forests of the Atlantic part of Europe, while being less abundant in beech forests of more continental parts of Europe, from Germany to the east and south. Close to the northern edge of its range, *M. effusum* occurs in small deciduous forest patches within a subarctic tundra matrix. Across 1220 repeat survey vegetation plots from deciduous forests across Europe, *M. effusum* increased in abundance by 2.1% during the last decades (De Frenne *et al.*, 2013b), which shows that within-range plant frequency changes are actually happening in nature in this species. *M. effusum* is wind-pollinated, typically produces 100–300 caryopses (hereafter referred to as ‘seeds’) per yr and per shoot (hereafter referred to as ‘individual’), and also develops short stolons for vegetative spread (Tyler, 2002; De Frenne *et al.*, 2011b). Regeneration from seed is the most important means of population persistence and spread (Tyler, 2002). Seeds are mainly gravity-dispersed, but myrmecochory, epizoochory and endozoochory occur as well (Graae, 2002; Heinken & Raudnitschka, 2002; von Oheimb *et al.*, 2005; Delatte & Chabrerrie, 2008), making the species a relatively fast colonizer compared with other forest understorey species (Brunet, 2007; Brunet *et al.*, 2012).

### Seed and soil collection

In 2011, seeds and soil samples were collected from 22 *M. effusum* populations in deciduous forests. The 22 populations were spread across a large part of the European distribution range of *M. effusum* (Fig. 1). The mean annual temperature across the sites ranged from 6.3 to 12.3°C while precipitation ranged from 553 to 1091 mm yr<sup>-1</sup> (Supporting Information, Table S1). To exclude covariation between temperature and tree species effects such as leaf litter quality and other environmental variables, we focused on temperate beech (dominant tree species *Fagus sylvatica*; 16 sites) and oak forests (*Quercus robur*; six sites) on relatively acidic soils. The mean topsoil pH measured in KCl was 3.8 (see later and Table S1). The forests were most probably ancient – there were no cartographical or other historical records of agricultural land use for at least 150 yr – thus avoiding land-use effects on soil properties (Verheyen *et al.*, 1999). There had been no recent stand-replacing management actions such as clear-cuts (tree age > 50 yr) and total canopy cover was at least 50%. Apart from *M. effusum*, the understorey vegetation mainly consisted of species such as *Oxalis acetosella*, *Luzula pilosa*, *Maianthemum bifolium*, *Rubus fruticosus* agg., *Convallaria majalis*, *Galium odoratum*, *Mercurialis perennis*, *Carex pilosa*, *Dentaria bulbifera* and *Anemone nemorosa*. In each site, we

selected a 5 × 5 m<sup>2</sup> plot that was homogeneous in terms of the light environment, structure of the herbaceous layer and other environmental variables, and from within it collected all the seeds of 15 randomly selected *M. effusum* individuals at the time of seed maturity (May–September 2011; Table S1). The seeds were stored dry at room temperature until sowing. Within the same plots, after removing the litter layer, c. 31 of fresh mineral soil (0–10 cm topsoil) was collected between late September and early November 2011. To minimize the consequences of soil disturbance, the soil was kept at 2°C until the installation of the experiment. All soil samples were then passed through a 4 mm sieve to homogenize the soil and remove most roots and stones.

### Experimental design

We used combinations of seeds and soils corresponding to virtual movement scenarios (see Reich & Oleksyn (2008) and Baldwin *et al.* (2013) for analogous applications) of up to 1600 km, both northward (as immigrants are expected to track the shifting isotherms and thus to be drawn from currently warmer sites) and southward (which can occur stochastically or, for instance, as a result of competitive release as a result of land-use changes; Lenoir *et al.*, 2010). Therefore, seeds from each of the 22 sites were sown in their local soil and, in addition, seeds collected from three sites (in northern Belgium, southern Poland and southern Sweden; red circles in Fig. 1, henceforth referred to as ‘migrant populations’) were sown into the other, nonlocal soils. For instance, the seeds of migrant population no. 12 were sown in soil from site 12 and in nonlocal soil from the 21 other sites; a similar approach was followed for seeds of migrant populations numbers 11 and 19 (Fig. 1). These virtually migrant populations were selected based on their geographical position across the distribution range (i.e. avoiding the periphery of the species’ range). Pots (6.8 cm<sup>2</sup> surface area × 4.4 cm depth) were filled with the soil of each site between 9 and 11 November 2011 and left in the same glasshouse for 1 wk of preincubation. Between 16 and 18 November 2011, each seed provenance was randomly assigned to a pot (five seeds per pot) and each pot was randomly assigned to treatments of temperature (cool and warm glasshouse) and light availability (ambient light and shaded by shading cloth). This design resulted in a total of 1408 pots: 22 sites × four seed provenances for each soil provenance × two light treatments × two temperatures × four replicates. The pot positions were shifted randomly on a weekly basis within each treatment and watered with distilled water. By using this experimental setup, we excluded the longer-term effects of understorey plant–plant interactions and specifically focused on the importance of nonlocal soils in shaping plant establishment as climate changes.

Warming was achieved by using temperature-controlled glasshouses at two temperatures: a cool glasshouse with minimum night-time temperature set to 10°C and a warm glasshouse with minimum night-time temperature set to 15°C. The actual temperature was monitored using temperature sensors installed in the pots and connected to data loggers logging at 15 min intervals (Decagon Inc., Pullman, WA, USA). The actual mean temperature during the experiment in the cool treatment was 11.6°C,

whereas the mean temperature in the warming treatment was 15.3°C (3.7°C warmer; see Fig. S1 for detailed temperature data). This temperature increase is comparable to predicted mean temperature increases in northern Europe by the end of this century (3.2°C; IPCC, 2007).

The shade cloth used for the irradiance treatments was installed c. 30 cm above the plants and gradually raised with plant canopy growth. To quantify the light reduction resulting from the shade cloth, the photosynthetically active radiation (PAR) was measured on 6 d (both sunny and uniformly cloudy) between December 2011 and March 2012 under the shade cloth and above the controls between 10:30 h and 14:00 h using a Skye Instruments (Llandrindod Wells, UK) PAR Quantum sensor connected to a Spectrosense 2+ meter (10 paired measurements per occasion). The mean PAR was reduced by 94.5% ( $SD = 0.94$ ) below the shade cloth relative to the ambient irradiance values (average ambient PAR was  $36 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), reflecting realistic forest understorey light intensities after canopy flush (Augspurger *et al.*, 2005). The shaded and ambient light treatments are further referred to as 'shading' and 'simulated canopy opening', respectively.

### Chemical soil analyses and seed bank

Before the experiment, additional soil from each site was dried at 40°C for 48 h, passed through a 2 mm sieve and analysed for pH (determined from a solution of 14 ml dry soil in 70 ml 1 M KCl with a glass electrode), bioavailable phosphorus (P; Olsen extraction with 0.5 M NaHCO<sub>3</sub> at pH 8.5 and colorimetric determination), exchangeable calcium (Ca), potassium (K) and magnesium (Mg) (extraction with 0.1 M BaCl<sub>2</sub> and atomic absorption spectroscopy) and total carbon (C) and nitrogen (N) (elemental analyser). We calculated the C : N ratio by dividing the total C by the N percentage. To quantify extractable N as ammonium and nitrate, KCl extractions of the soil were performed by shaking an extra subsample of c. 30 g fresh soil per site in 60 ml 1 M KCl for 1 h. This solution was filtered, and ammonium and nitrate concentrations were determined colorimetrically on an autoanalyzer by the salicylate-nitroprusside method (ammonium) and reduction of nitrate to nitrite in a Cu-Cd column followed by the reaction of nitrite with *N*-(1-naphthyl)ethylenediamine dihydrochloride to produce a chromophore (nitrate). Supplementary soil was installed in 12 similar pots per soil provenance (but without seed sowing) under both temperature treatments to quantify seed bank recruitment of *M. effusum* (which could be confused with germination of sown seeds). Seed bank recruitment of *M. effusum* was found to be negligible: only four and seven seedlings emerged from the 264 pots without seed sowing (12 pots  $\times$  22 soil provenances) in the cool and warm treatments, respectively, compared with 3969 seedlings in the 1408 pots with seed sowing used in further analyses.

### Environmental variables

Eighteen geographical, biological, climatic and pedological environmental variables were compiled for each of the 22 sites:

latitude and longitude of the plots (°), visually estimated average tree canopy cover above the plot (%), average thickness of the litter layer inside the plot (cm), and soil characteristics (soil pH, P, K, Ca, Mg, total C and N, C : N ratio, and extractable N – recorded in terms of ammonium, nitrate, and ammonium + nitrate). Additionally, the mean annual near-surface air temperature and precipitation (1981–2000) for each site were compiled through FetchClimate (Microsoft Research Cambridge, <http://fetchclimate.cloudapp.net>), a web application that chooses the most accurate source for each particular climate variable (WorldClim in this case, Hijmans *et al.*, 2005). The mean annual temperature was significantly correlated with the April–September growing season temperature ( $r=0.782$ ,  $n=22$ ,  $P<0.001$ ). Atmospheric N deposition as the sum of wet and dry depositions of reduced (NH<sub>x</sub>) and oxidised (NO<sub>y</sub>) N was calculated based on modelled EMEP deposition data for 2009 ([http://webdab.emep.int/Unified\\_Model\\_Results](http://webdab.emep.int/Unified_Model_Results)). Estimated N deposition rates varied between 4.5 kg N ha<sup>-1</sup> yr<sup>-1</sup> (central Sweden) and 23.2 kg N ha<sup>-1</sup> yr<sup>-1</sup> (northwestern Germany and the Netherlands).

### Plant measurements

The number of seedlings (visible emerged shoots) was recorded regularly throughout the experiment (20, 29, 34, 55, 76 and 154 d after sowing). On 12–17 April 2012, the experiment was terminated. Plant height was measured from the soil surface to the top of the plant. The final emergence percentage (calculated as the number of plants at the end of the experiment divided by the original seed input) was determined, and the above-ground and below-ground biomass harvested separately. Subsequently, the biomass per pot was divided by the number of plants to determine the biomass per plant. All biomass samples were dried for 72 h at 70°C and weighed. Root : shoot (R : S) ratios were calculated as the below-ground biomass divided by the above-ground biomass, and total biomass as the sum of above-ground and below-ground biomass. The mean emergence time was calculated as (Ranal & De Santana, 2006):

$$\sum_1^i \frac{n_i t_i}{N}$$

where  $n_i$  is the number of emerged seedlings within consecutive time intervals,  $t_i$  is the time between the beginning of the experiment and the end of a time interval (in wk), and  $N$  is the final number of emerged seedlings per pot.

### Data analysis

To quantify virtual plant movements, we analysed the effects of the temperature difference ( $\Delta\text{Temp}$ ) between the sites of seed and soil collection corresponding to potential movement scenarios of plant populations in the face of climate warming ('mean temperature transfer distance' *sensu* Reich & Oleksyn, 2008). As distance metrics or latitudinal positions as such are not meaningful for plant growth (Körner, 2007; De Frenne *et al.*, 2013a), we

express this difference in temperature units ( $^{\circ}\text{C}$ ) rather than degrees of latitude or km.  $\Delta\text{Temp}$  was calculated as the mean annual temperature of the site of seed collection minus the temperature of the site of soil collection, such that positive values correspond to a ‘coldward’ movement scenario (i.e. mainly to the north, as expected with climate warming), whilst negative values refer to a ‘warmward’ movement scenario (mainly to the south).

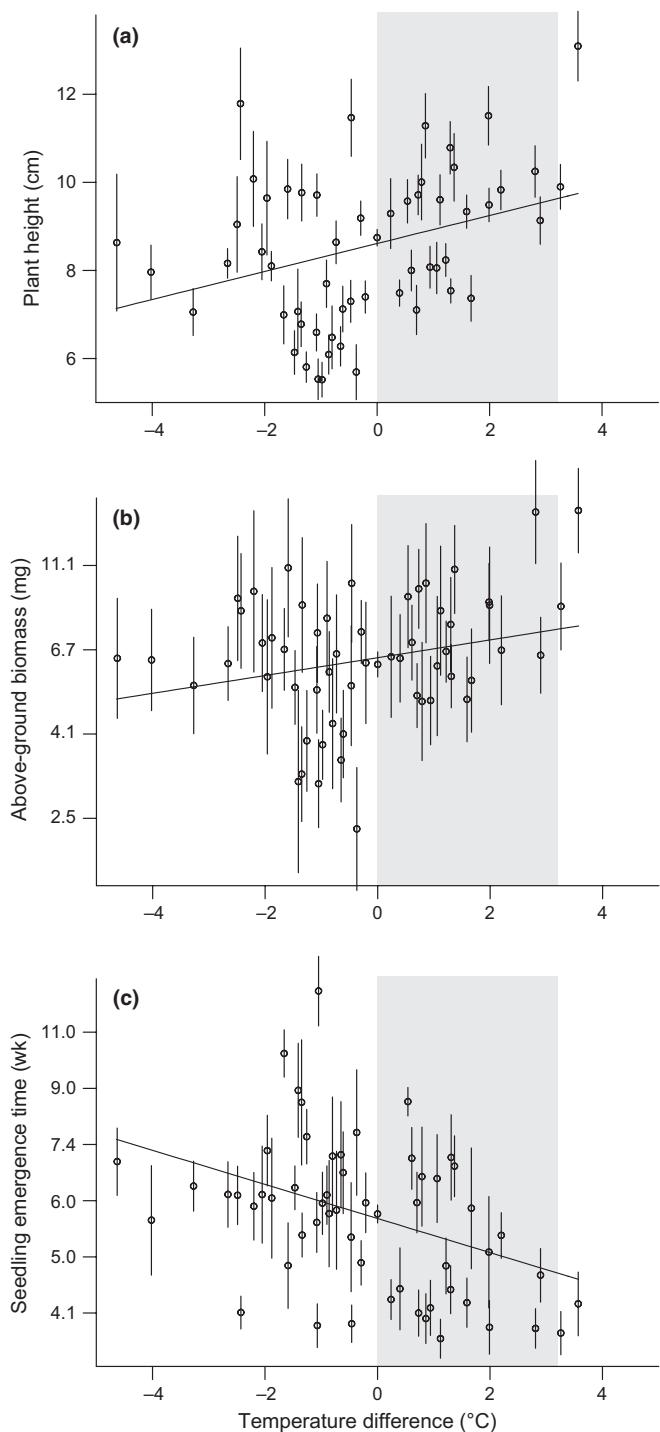
The effects of  $\Delta\text{Temp}$  and the experimental treatments of warming and simulated canopy opening on the seedling emergence and growth of *M. effusum* plants were assessed through linear mixed-effect models with ‘site’ as random-effect term using the lme function in the nlme package (for height, biomass, R : S ratio and emergence time data). Before the analyses, biomass, R : S ratio and emergence time data were log-transformed to meet the normality assumption of the statistical tests. For emergence percentages, generalized linear mixed-effect models were applied throughout the analyses using the lmer function in the lme4 package with binomial errors and the logit link function (Zuur *et al.*, 2009). All analyses were performed in R 3.0.1 (R Core Team, 2013).

Subsequently, to explain  $\Delta\text{Temp}$  effects on seedling emergence and plant growth, the relationships between the temperature difference  $\Delta\text{Temp}$  and changes in the other environmental factors between the sites of seed and soil collection ( $\Delta\text{Env}$ ) were calculated by means of Pearson correlations. Analogous to  $\Delta\text{Temp}$ ,  $\Delta\text{Env}$  was calculated as the value of the environmental factor at the site of seed collection minus the value of the environmental factor at the site of soil collection. Positive  $\Delta\text{Env}$  values for N deposition, for example, correspond to a movement scenario towards sites with lower N deposition, and vice versa. The effects of  $\Delta\text{Env}$  on seedling emergence and plant growth were assessed using similar mixed-effect models as for  $\Delta\text{Temp}$  (i.e. models including  $\Delta\text{Env}$ , ‘warming’ and ‘canopy opening’ as fixed factors, but only the effects of  $\Delta\text{Env}$  are reported to avoid overlap with the first analysis).

To determine the degree of local soil advantage, seedling emergence and plant growth of seeds sown in their local soil were compared with those of seeds from the three migrant populations in nonlocal soils. We therefore evaluated ‘seed origin’ (four levels; i.e. sown in local soil, and seeds of the three migrant populations in nonlocal soils) as a factor in mixed-effect models with *site* as random-effect term as above. Multiple comparisons (Tukey *post hoc* test) were performed with the glht function in the multcomp package in R.

## Results

We found significant positive effects of the temperature difference between the sites of seed and soil collection ( $\Delta\text{Temp}$ ) on height and above-ground and total biomass of *M. effusum*, and significant negative effects on the seedling emergence time (Fig. 2; Table 1). Thus, *M. effusum* individuals grew taller and produced more biomass when virtually dispersed to soils coming from colder sites than the seed origin. Below-ground biomass, R : S ratio and emergence percentage did not show a significant relationship with  $\Delta\text{Temp}$ .



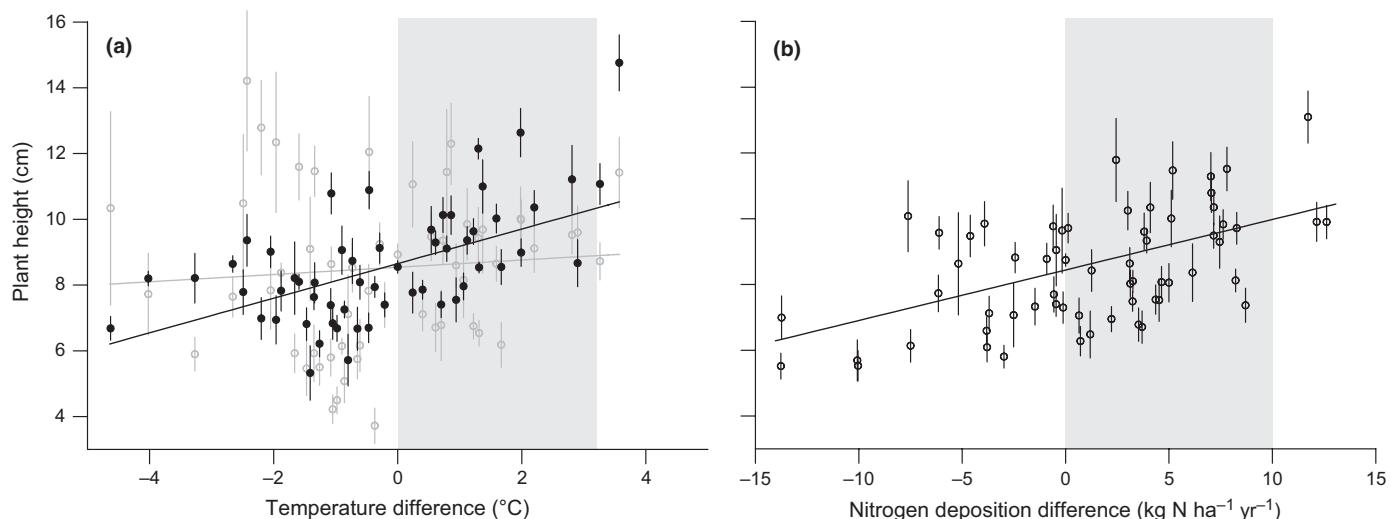
**Fig. 2** Relationships between the temperature difference between the sites of seed and soil collection and the plant height (a), above-ground biomass (b) and emergence time (c) of *Milium effusum*. The fitted lines depict significant relationships from mixed-effect models and shaded areas reflect seeds transferred to soils currently 0–3.2°C colder (+3.2°C corresponds to the mean warming predicted for northern Europe by the end of this century; IPCC, 2007). Each circle represents a mean (error bars denote  $\pm \text{SE}$ ) per seed  $\times$  soil provenance combination for visualization, but pot-level data were used for the statistical analyses using mixed-effect models that take the hierarchical nature of the data into account (Table 1). Note the log-transformed y-axis for biomass and emergence time.

Experimental warming had positive effects on plant height, above-ground and total biomass and emergence percentages, but decreased below-ground biomass, R : S ratio and emergence time of *M. effusum* (Table 1). Simulated canopy opening increased biomass and R : S ratios, and decreased the emergence percentage and emergence time. The interactive effect of canopy opening and warming was significant for plant height, emergence percentage and emergence time, indicating differential effects of temperature under varying light conditions. Importantly, there were very few significant interactive effects between  $\Delta\text{Temp}$ , on the one hand, and warming and canopy opening on the other hand. Only light availability had a strong interactive effect on the relationship between  $\Delta\text{Temp}$  and plant height of *M. effusum* (Table 1), with a positive effect of  $\Delta\text{Temp}$  on the height of shaded plants and no significant relationship for plants under simulated canopy opening (Fig. 3a).

**Table 1** Effects of the temperature difference between the sites of seed and soil collection ( $\Delta\text{Temp}$ ) and warming and simulated canopy opening on seedling emergence and plant growth of *Milium effusum*

	$\Delta\text{Temp}$	Warming	Canopy opening	$\Delta\text{Temp}$ : canopy	$\Delta\text{Temp}$ : warming	Warming: canopy	Warming: canopy: $\Delta\text{Temp}$
Plant height	↑6.0*	140.8***	ns	17.7***	ns	39.0***	ns
Above-ground biomass	↑4.0*	↑79.6***	↑2372.2***	ns	ns	ns	ns
Below-ground biomass	ns	↓4.6*	↑3190.9***	ns	ns	3.1(*)	ns
Total biomass	↑3.0(*)	↑7.2**	↑3679.0***	ns	ns	ns	ns
Root : shoot ratio	ns	↓130.8***	↑258.9***	3.1(*)	ns	ns	ns
Emergence	ns	↑13.3***	↓4.4***	ns	-2.6*	-3.4***	ns
Emergence time	↓10.3**	↓1258.4***	↓52.7***	ns	ns	53.7***	ns

Values are *F*-values (z-values for emergence) from mixed-effect models ( $n = 1408$ ). The model coefficients are available in Table S2. The direction of the effect is given: ↑ corresponds to an increase in the trait value with increasing  $\Delta\text{Temp}$  and with warming or canopy opening, whereas ↓ corresponds to the opposite pattern. Significance: ns, nonsignificant ( $P > 0.1$ ); \*,  $P < 0.1$ ; \*\*,  $P < 0.05$ ; \*\*\*,  $P < 0.01$ ; \*\*\*\*,  $P < 0.001$ .



**Fig. 3** Relationships between the plant height of *Milium effusum* and: (a) the temperature difference between the sites of seed and soil collection for shaded plants (closed circles; mixed-effect model,  $F = 22.4$ ,  $P < 0.001$ ) and under simulated canopy opening (open circles;  $F = 0.32$ ,  $P = 0.570$ ); (b) the nitrogen deposition difference between the sites of seed and soil collection (the interaction with light was not significant for this variable; mixed-effect model,  $P = 0.995$ ). The fitted lines depict relationships from mixed-effect models and shaded areas reflect seeds transferred to soils currently 0–3.2°C colder (+3.2°C corresponds to the mean warming predicted for northern Europe by the end of this century; IPCC, 2007) or soils experiencing N deposition values 0–10  $\text{kg N ha}^{-1} \text{yr}^{-1}$  lower. Each circle represents a mean (error bars denote  $\pm \text{SE}$ ) per soil  $\times$  seed provenance combination for visualization, but pot-level data were employed for the statistical analyses using mixed-effect models that take the hierarchical nature of the data into account (Tables 1 and 3).

The temperature difference between the sites of seed and soil collection was correlated with concurrent changes in several of the investigated environmental variables ( $\Delta\text{Env}$ ; Table 2). Most significantly,  $\Delta\text{Temp}$  increased with increasingly positive precipitation, N deposition, soil pH, and K and Ca concentration differences between the sites of seed and soil collection ( $\Delta\text{Env}$  values). In other words, positive  $\Delta\text{Temp}$  values correspond to a ‘cold-ward’ movement scenario, but also reflect movements towards sites, for instance, with lower N deposition and soil pH within our study area. Accordingly, positive  $\Delta\text{Env}$  values for N deposition, soil pH and base cation concentrations had a significantly positive effect on plant height and above-ground and total biomass (N deposition only), and a negative effect on the emergence time (Fig. 3b; Table 3). Increasingly positive soil pH and base cation concentration  $\Delta\text{Env}$  values also resulted in higher emergence percentages. Therefore, N deposition and soil pH emerge

as most important among the studied environmental variables affecting migrant populations of this species.

When the three moving populations in nonlocal soils were compared with home-sown plants, we found significant differences in seedling emergence and plant growth (Table 4). The plants sampled in site no. 12 in Belgium were tallest and produced most above-ground biomass, while the plants sampled in site no. 11 in Poland were the smallest. Emergence was lowest (mean emergence 51%) but fastest (mean emergence time 4.8 wk) for the seeds sampled in site no. 12 and highest (68%) yet slowest (8.7 wk) for the seeds sampled in site no. 11. There were few obvious advantages of growing on local soil: the performance of seeds grown on local soil was middle ranking for all investigated traits except for the R : S ratio.

## Discussion

Plant colonization consists of two steps: dispersal of diaspores and, subsequently, establishment. Most plants are immobile for most of their life cycle but may track their shifting climatic envelope during seed dispersal as climate changes. To be able to predict future plant movements, it is therefore critical not only to evaluate seed dispersal through the landscape (Corlett & Westcott, 2013), but also to test how individuals originating from different thermal environments can establish in nonlocal sites after dispersal (Engelkes *et al.*, 2008; Ibanez *et al.*, 2009; van der Putten *et al.*, 2010). Using continental-scale sampling of seeds and soils subjected to a combination of two temperature and irradiance treatments, we were able to test realistic scenarios anticipated under projected climate warming. More specifically, we experimentally tested the establishment phase by quantifying

**Table 2** Relationships between the temperature difference ( $\Delta\text{Temp}$ ) and differences in the other environmental variables between the sites of seed and soil collection ( $\Delta\text{Env}$ )

Environmental variable ( $\Delta\text{Env}$ )	r	P
Latitude	-0.635	< 0.001
Longitude	-0.671	< 0.001
Precipitation	0.359	0.003
N deposition	0.549	< 0.001
Canopy cover	-0.167	ns
Litter thickness	-0.137	ns
Soil pH	0.443	< 0.001
Soil P	0.154	ns
Soil K	0.305	0.013
Soil Mg	0.078	ns
Soil Ca	0.367	0.002
Extractable soil $\text{NH}_4^+$	-0.036	ns
Extractable soil $\text{NO}_3^-$	0.005	ns
Total extractable soil N	-0.036	ns
Total soil N	-0.212	0.087
Total soil C	-0.157	ns
Soil C : N	0.200	ns

Positive Pearson correlation coefficients denote a decrease in the environmental variable from the site of seed collection to the site of soil collection (i.e. positive  $\Delta\text{Env}$ ) with increasing  $\Delta\text{Temp}$ , and vice versa (22 soil provenances  $\times$  three migrating populations = 66 combinations).

intraspecific variation in growth responses to nonlocal soils that plants are expected to experience in the future.

We found the height and above-ground and total biomass of *M. effusum* to increase as a function of the temperature difference between the sites of seed and soil collection ( $\Delta\text{Temp}$ ). Thus, *M. effusum* tends to grow significantly taller and produce more biomass when transplanted to soils coming from colder sites than the seed origin. In addition, emergence of seedlings accelerated when sown into soil coming from colder sites than the seed origin. These findings suggest that migrant *M. effusum* populations might encounter increasingly favourable soil conditions while tracking the shifting isotherms. The effects of  $\Delta\text{Temp}$  are also not affected by the experimental temperature treatment, as indicated by the mainly insignificant interactions between  $\Delta\text{Temp}$  and the warming treatment. This suggests that a positive effect of soil conditions on plant performance would persist even under conditions where plants and soils are influenced by increasing temperatures, at least in the short term.

Direct experimental warming also increased the performance and seedling emergence rates of *M. effusum*. The predicted climatic changes (IPCC, 2007) thus have the potential to significantly improve growth and accelerate seedling emergence of this species, not only by directly affecting plant performance (cf. De Frenne *et al.*, 2012), but also indirectly through positive plant–soil feedbacks during migration. Shorter emergence times as a result of direct warming are probably related to faster embryo development and epicotyl growth under higher temperatures (Walck *et al.*, 2011). Earlier seedling emergence can be beneficial to plants when it results in more time available for resource allocation to perennating organs before winter and/or accelerated leaf development during the next spring (Cook, 1980), but harmful if it results in more frost damage. The former is particularly relevant for forest understorey plants that try to exploit the period of high light availability in spring as much as possible, and avoid the period of extensive canopy shade in summer (Augspurger *et al.*, 2005). We also found slower seedling emergence as a result of shading, which can be attributed to the controlling effect of red-to-far red (R : FR) light ratios on germination of understorey species such as *M. effusum* (Jankowska-Blaszcuk & Daws, 2007). The R : FR ratio of light below shade cloth tends to be slightly lower than in full sunlight (McMahon *et al.*, 1990), thereby moving the light conditions towards those experienced at the forest floor (Daws *et al.*, 2002). Climate warming may also alter shading and light availability at the forest floor by affecting growth and composition of the tree layer (McMahon *et al.*, 2010; Hanelinkel *et al.*, 2013).

We propose two complementary explanations for the enhanced growth of *M. effusum* transplanted to soils coming from colder sites than the seed origin. Forest soils from colder sites tend to differ biogeochemically from warmer ones in our dataset mainly in terms of experienced N deposition rates, soil pH, and soil K and Ca concentrations, and these environmental factors also correlated best with plant growth and seedling emergence. Therefore, a first mechanism that may explain the increased performance of plants transplanted to soils of colder sites is that mycorrhizal occurrence in the soil generally decreases

**Table 3** Effects of environmental differences between the sites of seed and soil collection ( $\Delta\text{Env}$ ) on seedling emergence and plant growth of *Milium effusum*

Environmental variable ( $\Delta\text{Env}$ )	Plant height	Above-ground biomass	Below-ground biomass	Total biomass	Root : shoot ratio	Emergence	Emergence time
Latitude	↓3.1(*)	ns	ns	ns	↑8.1**	ns	ns
Longitude	↑6.5*	ns	↑5.1*	↑4.1*	ns	↓-2.1*	↑12.1***
Precipitation	↑5.6*	ns	ns	ns	↓5.3*	ns	ns
N deposition	↑17.4***	↑9.7**	ns	↑4.7*	↓5.5*	ns	↓23.9***
Canopy cover	ns	ns	ns	ns	↑7.7**	ns	↑6.1*
Litter thickness	↓3.8(*)	ns	ns	ns	ns	↓-2.2*	↑7.4**
Soil pH	↑6.4*	ns	ns	ns	ns	↑2.1*	↓16.9***
Soil P	ns	ns	ns	ns	↑5.4*	↑2.3*	↓11.7***
Soil K	↑4.5*	ns	ns	ns	ns	↑2.8**	↓16.2***
Soil Mg	ns	ns	ns	ns	ns	↑1.9(*)	ns
Soil Ca	↑7.2**	ns	ns	ns	↓4.7*	ns	↓12.5***
Extractable soil $\text{NH}_4^+$	ns	ns	↓3.9(*)	ns	ns	ns	ns
Extractable soil $\text{NO}_3^-$	↓2.9(*)	ns	ns	ns	ns	ns	↑4.4*
Total extractable soil N	ns	ns	↓3.3(*)	ns	ns	ns	ns
Total soil N	ns	ns	ns	ns	ns	↑1.7(*)	ns
Total soil C	ns	ns	ns	ns	ns	↑2.2*	ns
Soil C : N	ns	ns	ns	ns	ns	ns	ns

Values are  $F$ -values (z-values for emergence) from mixed-effect models ( $n = 1408$ ). The direction of the effect is given: ↑ corresponds to an increase in the trait value with increasing  $\Delta\text{Env}$ , whereas ↓ corresponds to a decrease. Significance: ns, nonsignificant ( $P > 0.1$ ); (\*),  $P < 0.1$ ; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

with N deposition (Gilliam, 2006; Bobbink *et al.*, 2010). Soil sampled from sites with higher mean temperatures (southerly in our study sites) tends to have experienced relatively high amounts of N deposition, which may have decreased mycorrhizal occurrence and subsequent mycorrhizal colonization on *M. effusum* roots, nutrient acquisition and growth in forest soils from warmer sites compared with soils from colder sites. Secondly, the positive plant responses in soils from currently colder sites might be related to lower soil pathogenic activity in acidic soils and colder regions (e.g. Brasier, 1996; Jönsson *et al.*, 2003; van der Putten *et al.*, 2010; Roos *et al.*, 2011). Plant individuals may, at least temporarily, be released from soil pathogens following climate change-driven range expansion as a result of lower dispersal rates of below-ground organisms (van Grunsven *et al.*, 2007, 2010; Engelkes *et al.*, 2008; Berg *et al.*, 2010; van der Putten *et al.*,

2010). Enemy release, for example, is well known to improve growth of invasive plant species in their invaded range (Reinhart *et al.*, 2003; Callaway *et al.*, 2004; Wolfe & Klironomos, 2005). Movement towards soils from currently colder sites with lower pathogen loads might therefore enhance plant growth (van Grunsven *et al.*, 2010). Furthermore, corroborating this hypothesis, the positive relationship between  $\Delta\text{Temp}$  and plant height disappeared under simulated canopy opening. In this case, higher assimilation capacity under high light availability might have compensated for biomass reduction from soil pathogens. As below-ground organisms probably have lower potential dispersal rates than plants as climate changes (Berg *et al.*, 2010), lags between contrasting trophic levels can be expected. Therefore, determining the specific effects of the soil and plant community that migrant plant populations might experience should be a

**Table 4** Effects of the seed origin on seedling emergence and plant growth of *Milium effusum* sown in their local soil and of the migrant populations in nonlocal soils

	Seed × soil origin				$F$ or $\chi^2$	$P$
	Local soil	Nonlocal soil				
		Belgium (site no. 12)	Poland (site no. 11)	Sweden (site no. 19)		
Plant height (cm)	8.75 (0.19) ab	9.98 (0.16) a	7.59 (0.13) b	7.88 (0.18) b	8.6	<0.001
Above-ground biomass (mg)	15.7 (1.1) ab	16.2 (1.1) a	11.2 (0.8) b	15.2 (1.3) ab	2.9	0.042
Below-ground biomass (mg)	19.1 (1.3)	22.5 (1.8)*	15.0 (1.2)*	24.8 (2.1)	2.5	0.066
Total biomass (mg)	35.0 (2.3) ab	38.9 (2.8) a	26.3 (1.9) b	40.3 (3.3) ab	2.9	0.039
Root : shoot ratio	1.98 (0.25)	1.25 (0.05)	1.67 (0.16)	1.67 (0.09)	0.85	0.469
Emergence (%)	53.40 (1.6) b	51.19 (1.33) b	67.86 (1.56) a	53.63 (1.27) b	19.1	<0.001
Emergence time (wk)	7.26 (0.29) a	4.82 (0.14) b	8.65 (0.39) a	7.52 (0.23) a	13.2	<0.001

$F$ -values ( $\chi^2$  value for emergence) and  $P$ -values from mixed-effect models ( $n = 1408$ ). Values between brackets denote SE and different letters within the same row indicate significant differences ( $P < 0.05$ , or  $P < 0.10$  indicated by \*, Tukey post hoc test). The site numbers refer to the numbers in Fig. 1.

focus of future research (van der Putten *et al.*, 2010; Lau & Lennon, 2011). For instance, how longer-term competition from other understorey plant species influences migrants remains unclear.

Evidence from transplantation experiments of plants suggests that many species are capable of successfully growing and reproducing beyond their current distribution range limit (overview in Gaston, 2009). However, we provide a direct empirical test of the continent-wide performance of plants within the current distribution range. Large-scale transplant experiments generally found indications of local adaptation, that is, increased performance of plants replanted at the home site compared with plants transplanted at distant sites (Joshi *et al.*, 2001; Etterson, 2004; Macel *et al.*, 2007; De Frenne *et al.*, 2011a). Climate and soil characteristics are key agents that may contribute significantly to selection processes and lead to local adaptation in plants (Linhart & Grant, 1996; Macel *et al.*, 2007; Grondahl & Ehlers, 2008; De Frenne *et al.*, 2011a; Ågren & Schemske, 2012). Yet, the specific contribution of environmental variables (climate, soil and other factors) to the differences in selection regimes across sites is difficult to unravel in conventional field-based transplant experiments (Macel *et al.*, 2007). Here, we provided such a test by specifically focusing on adaptation to abiotic and biotic soil characteristics, and found no evidence of home-soil advantages. The evidence provided here instead highlights the role of soil biota in plant performance (see earlier).

In summary, while tracking climate warming, migrant plant populations will probably experience increasingly dissimilar non-climatic environmental conditions, as lag effects at other levels of biological organisation can be expected (Berg *et al.*, 2010; van der Putten *et al.*, 2010). Here we show that experimental *M. effusum* movements towards soils from currently colder sites resulted in increased plant height, above-ground and total biomass and accelerated seedling emergence. These results suggest that seedling emergence may accelerate and growth increase when *M. effusum* populations from currently warmer sites migrate towards currently colder sites. We stress that, while we only accounted for changing soil characteristics for migrant populations, these alone affected seedling establishment and plant growth considerably. Nonlocal soil characteristics and below-ground biotic interactions might thus be key to the establishment of migrants (van Grunsven *et al.*, 2007; Engelkes *et al.*, 2008) and shape climate change-driven movement of plant populations in the future. The importance of such intraspecific variation for population and community dynamics is increasingly being recognized (Viole *et al.*, 2012; Pauls *et al.*, 2013) and should be incorporated into predictions on future range shifts of species, as establishment is an essential step in the colonization process of plants.

## Acknowledgements

We thank the Research Foundation – Flanders (FWO) for funding the scientific research network FLEUR ([www.fleur.ugent.be](http://www.fleur.ugent.be)). We are also grateful to Cristina Blandino, Pete Michna, Luc Willems and Greet De bruyn for field, laboratory and technical assistance. Support for this work was provided by FWO postdoctoral

fellowships (to P.D.F. and A.D.S.), the Special Research Fund of Ghent University (to R.G.) and long-term research project RVO 67985939 (to R.H. and P.P.).

## References

- Ågren J, Schemske DW. 2012. Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist* 194: 1112–1122.
- Augspurger CK, Cheeseman JM, Salk CF. 2005. Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. *Functional Ecology* 19: 537–546.
- Baldwin AH, Jensen K, Schönfeldy M. 2013. Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. *Global Change Biology*. doi: 10.1111/gcb.12378.
- Berg MP, Kiers ET, Driessen G, Van der Heijden M, Kooi BW, Kuenen F, Liefing M, Verhoef HA, Ellers J. 2010. Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology* 16: 587–598.
- Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F *et al.* 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20: 30–59.
- Brasier CM. 1996. *Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change. *Annales des Sciences Forestières* 53: 347–358.
- Brunet J. 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* 44: 563–572.
- Brunet J, De Frenne P, Holmstrom E, Mayr ML. 2012. Life-history traits explain rapid colonization of young post-agricultural forests by understory herbs. *Forest Ecology and Management* 278: 55–62.
- Callaway RM, Thelen GC, Rodriguez A, Holben WE. 2004. Soil biota and exotic plant invasion. *Nature* 427: 731–733.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.
- Cook RE. 1980. Germination and size-dependent mortality in *Viola blanda*. *Oecologia* 47: 115–117.
- Corlett RT, Westcott DA. 2013. Will plant movements keep up with climate change? *Trends in Ecology & Evolution* 28: 482–488.
- Daws MI, Burslem DFRP, Crabtree LM, Kirkman P, Mullins CE, Dalling JW. 2002. Differences in seed germination responses may promote coexistence of four sympatric *Piper* species. *Functional Ecology* 16: 258–267.
- De Frenne P, Brunet J, Shevtsova A, Kolb A, Graae BJ, Chabrierie O, Cousins SAO, Decocq G, De Schrijver A, Diekmann M *et al.* 2011a. Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology* 17: 3240–3253.
- De Frenne P, Graae BJ, Brunet J, Shevtsova A, De Schrijver A, Chabrierie O, Cousins SAO, Decocq G, Diekmann M, Hermy M *et al.* 2012. The response of forest plant regeneration to temperature variation along a latitudinal gradient. *Annals of Botany* 109: 1037–1046.
- De Frenne P, Graae BJ, Kolb A, Shevtsova A, Baeten L, Brunet J, Chabrierie O, Cousins SAO, Decocq G, Dhondt R *et al.* 2011b. An intraspecific application of the leaf-height-seed ecology strategy scheme to forest herbs along a latitudinal gradient. *Ecography* 34: 132–140.
- De Frenne P, Graae BJ, Rodríguez-Sánchez F, Kolb A, Chabrierie O, Decocq G, De Kort H, De Schrijver A, Diekmann M, Eriksson O *et al.* 2013a. Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology* 101: 784–795.
- De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J *et al.* 2013b. Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences, USA* 110: 18561–18565.

- Delatte E, Chabrerie O. 2008. Seed dispersal efficiency of forest herbaceous plant species by the ant *Myrmica ruginodis*. *Comptes Rendus Biologies* 331: 309–320.
- Diffenbaugh NS, Field CB. 2013. Changes in ecologically critical terrestrial climate conditions. *Science* 341: 486–492.
- Engelkes T, Morrien E, Verhoeven KJF, Bezemer TM, Biere A, Harvey JA, McIntyre LM, Tamis WLM, Van der Putten WH. 2008. Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature* 456: 946–948.
- Etterson JR. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. 1. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution* 58: 1446–1458.
- Gaston KJ. 2009. Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences* 276: 1395–1406.
- Gilliam FS. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology* 94: 1176–1191.
- Graae BJ. 2002. The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Science Research* 12: 113–120.
- Grondahl E, Ehlers BK. 2008. Local adaptation to biotic factors: reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. *Journal of Ecology* 96: 981–992.
- van Grunsven RHA, van der Putten WH, Bezemer TM, Berendse F, Veenendaal EM. 2010. Plant-soil interactions in the expansion and native range of a poleward shifting plant species. *Global Change Biology* 16: 380–385.
- van Grunsven RHA, van der Putten WH, Bezemer TM, Tamis WLM, Berendse F, Veenendaal EM. 2007. Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology* 95: 1050–1057.
- Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE. 2013. Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change* 3: 203–207.
- Heinken T, Raudnitschka D. 2002. Do wild ungulates contribute to the dispersal of vascular plants in Central European forests by epizoochory? A case study in NE Germany. *European Journal of Forest Research* 121: 179–194.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- Hultén E, Fries M. 1986. *Atlas of North European vascular plants: north of the Tropic of Cancer*. Königstein, Germany: Koeltz Scientific.
- Ibanez I, Clark JS, Dietze MC. 2009. Estimating colonization potential of migrant tree species. *Global Change Biology* 15: 1173–1188.
- IPCC. 2007. Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate change 2007: the physical science basis*. Cambridge, UK: Cambridge University Press.
- Jankowska-Blaszcuk M, Daws MI. 2007. Impact of red: far red ratios on germination of temperate forest herbs in relation to shade tolerance, seed mass and persistence in the soil. *Functional Ecology* 21: 1055–1062.
- Jönsson U, Jung T, Rosengren U, Nihlgård B, Sonesson K. 2003. Pathogenicity of Swedish isolates of *Phytophthora quercina* to *Quercus robur* in two different soils. *New Phytologist* 158: 355–364.
- Joshi J, Schmid B, Caldeira MC, Dimitrakopoulos PG, Good J, Harris R, Hector A, Huss-Danell K, Jumpponen A, Minns A et al. 2001. Local adaptation enhances performance of common plant species. *Ecology Letters* 4: 536–544.
- Kawecki TJ, Ebert D. 2004. Conceptual issues in local adaptation. *Ecology Letters* 7: 1225–1241.
- Körner C. 2007. The use of ‘altitude’ in ecological research. *Trends in Ecology & Evolution* 22: 569–574.
- Lau JA, Lennon JT. 2011. Evolutionary ecology of plant-microbe interactions: soil microbial structure alters selection on plant traits. *New Phytologist* 192: 215–224.
- Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3: e4010.
- Lenoir J, Gegout J-C, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Svenning J-C. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33: 295–303.
- Linhart YB, Grant MC. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* 27: 237–277.
- Machel M, Lawson CS, Mortimer SR, Smilauerova M, Bischoff A, Cremieux L, Dolezal J, Edwards AR, Lanta V, Bezemer TM et al. 2007. Climate vs. soil factors in local adaptation of two common plant species. *Ecology* 88: 424–433.
- McMahon MJ, Kelly JW, Decoteau DR. 1990. Spectral transmittance of selected greenhouse construction and nursery shading material. *Journal of Environmental Horticulture* 8: 118–121.
- McMahon SM, Parker GG, Miller DR. 2010. Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences, USA* 107: 3611–3615.
- von Oheimb G, Schmidt M, Kriebitzsch WU, Ellenberg H. 2005. Dispersal of vascular plants by game in northern Germany. Part II: Red deer (*Cervus elaphus*). *European Journal of Forest Research* 124: 55–65.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Parolo G, Rossi G. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. *Basic and Applied Ecology* 9: 100–107.
- Pauls SU, Nowak C, Balint M, Pfenniger M. 2013. The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology* 22: 925–946.
- Peñuelas J, Sardans J, Estiarte M, Aogaya R, Carnicer J, Coll M, Barbata A, Rivas-Ubach A, Lluisa J, Garbulsky M et al. 2013. Evidence of current impact of climate change on life: a walk from genes to the biosphere. *Global Change Biology* 19: 2303–2338.
- van der Putten WH, Macel M, Visser ME. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society B* 365: 2025–2034.
- R Core Team. 2013. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ranal MA, De Santana DG. 2006. How and why to measure the germination process? *Revista Brasileira Botânica* 29: 1–11.
- Reich PB, Oleksyn J. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters* 11: 588–597.
- Reinhart KO, Packer A, van der Putten WH, Clay K. 2003. Plant-soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecology Letters* 6: 1046–1050.
- Roos J, Hopkins R, Kvarneden A, Dixielius C. 2011. The impact of global warming on plant diseases and insect vectors in Sweden. *European Journal of Plant Pathology* 129: 9–19.
- Sherrard ME, Maherli H. 2012. Local adaptation across a fertility gradient is influenced by soil biota in the invasive grass, *Bromus inermis*. *Evolutionary Ecology* 26: 529–544.
- Smith DS, Schweitzer JA, Turk P, Bailey JK, Hart SC, Shuster SM, Whitham TG. 2012. Soil-mediated local adaptation alters seedling survival and performance. *Plant and Soil* 352: 243–251.
- Svenning J-C, Sandel B. 2013. Disequilibrium vegetation dynamics under future climate change. *American Journal of Botany* 100: 1266–1286.
- Tyler T. 2002. Geographic structure of genetic variation in the widespread woodland grass *Milium effusum* L. A comparison between two regions with contrasting history and geomorphology. *Genome* 45: 1248–1256.
- Verheyen K, Bossuyt B, Hermy M, Tack G. 1999. The land use history (1278–1990) of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. *Journal of Biogeography* 26: 1115–1128.
- Violle C, Enquist BJ, McGill BJ, Jiang LIN, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27: 244–252.
- Walck JL, Hidayati SN, Dixon KW, Thompson K, Poschlod P. 2011. Climate change and plant regeneration from seed. *Global Change Biology* 17: 2145–2161.
- Wolfe BE, Klironomos JN. 2005. Breaking new ground: soil communities and exotic plant invasion. *BioScience* 55: 477–487.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. *Mixed effect models and extensions in ecology in R*. Berlin, Germany: Springer.

## Supporting Information

Additional supporting information may be found in the online version of this article.

**Fig. S1** Temperature measurements during the experiment.

**Table S1** Characteristics of the 22 study sites

**Table S2** Coefficients of the models mentioned in Table 1

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