

RESEARCH PAPER

Individualistic responses of forest herb traits to environmental change

H. Blondeel¹ , M. P. Perring^{1,2}, E. De Lombaerde¹, L. Depauw¹, D. Landuyt¹, S. Govaert¹, S. L. Maes¹ , P. Vangansbeke¹, P. De Frenne¹  & K. Verheyen¹

¹ Forest & Nature Lab, Campus Gontrode, Faculty of Bioscience Engineering, Ghent University, Melle-Gontrode, Belgium

² Ecosystem Restoration and Intervention Ecology Research Group, School of Biological Sciences, the University of Western Australia, Crawley, WA, Australia

Keywords

vegetation cover; land-use legacies; temperate forest; intraspecific trait variation; plant height; specific leaf area; nitrogen deposition; climate change.

Correspondence

H. Blondeel, Forest & Nature Lab, Campus Gontrode, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle-Gontrode, Belgium
E-mail: haben.blondeel@ugent.be

Editor

D. Byers

Received: 9 October 2019; Accepted: 19 February 2020

doi:10.1111/plb.13103

ABSTRACT

- Intraspecific trait variation (ITV; *i.e.* variability in mean and/or distribution of plant attribute values within species) can occur in response to multiple drivers. Environmental change and land-use legacies could directly alter trait values within species but could also affect them indirectly through changes in vegetation cover. Increasing variability in environmental conditions could lead to more ITV, but responses might differ among species. Disentangling these drivers on ITV is necessary to accurately predict plant community responses to global change.
- We planted herb communities into forest soils with and without a recent history of agriculture. Soils were collected across temperate European regions, while the 15 selected herb species had different colonizing abilities and affinities to forest habitat. These mesocosms (384) were exposed to two-level full-factorial treatments of warming, nitrogen addition and illumination. We measured plant height and specific leaf area (SLA).
- For the majority of species, mean plant height increased as vegetation cover increased in response to light addition, warming and agricultural legacy. The coefficient of variation (CV) for height was larger in fast-colonizing species. Mean SLA for vernal species increased with warming, while light addition generally decreased mean SLA for shade-tolerant species. Interactions between treatments were not important predictors.
- Environmental change treatments influenced ITV, either *via* increasing vegetation cover or by affecting trait values directly. Species' ITV was individualistic, *i.e.* species responded to different single resource and condition manipulations that benefited their growth in the short term. These individual responses could be important for altered community organization after a prolonged period.

INTRODUCTION

Functional traits are morphological, physiological or phenological traits that affect growth, reproduction and survival of plants (Violle *et al.* 2007; Funk *et al.* 2017). Variations in functional traits related to leaf economics ('leaf'), growth ('height') and reproduction ('seed') have been associated with trade-offs that plant species make in order to compete for resources across environmental gradients (Westoby 1998; Borer *et al.* 2014; Reich 2014; Garnier *et al.* 2016; Díaz *et al.* 2016; Beckman *et al.* 2018). While many authors have focused on trait variation between species and how different environments influence this (Wright *et al.* 2017; Bruelheide *et al.* 2018), trait variation also occurs within species (Siefert *et al.* 2015; Fajardo & Siefert 2018). This intraspecific trait variation (ITV) can occur in response to environmental drivers (Albert *et al.* 2010; Jung *et al.* 2010) and is maintained through processes of phenotypic plasticity and genetic differentiation (Valladares *et al.* 2006). Phenotypic plasticity is an individual's plastic response to its environment, and its effect can be larger than that of genetic adaptation in altering trait values of species at small

spatiotemporal scales (Lajoie & Vellend 2015, 2018; Turcotte & Levine 2016). Changes in mean trait values of species in response to altered environments can ultimately affect variability in traits across populations, and thus contribute to ITV (Moran *et al.* 2016). Thus, ITV can significantly influence community patterns and processes (Bolnick *et al.* 2011; Escudero & Valladares 2016), and accounting for such effects improves predictions of future plant communities in a changing world (Laughlin *et al.* 2012; Cadotte *et al.* 2015).

Evidence exists that competition for light enhances ITV in height and leaf trait values (Le Bagousse-Pinguet *et al.* 2015; Bennett *et al.* 2016; Henneron *et al.* 2017). This is most evident in asymmetric competition for light, where light as a resource is disproportionately removed by individuals that manage to grow taller than their direct neighbours (Freckleton & Watkinson 2001). In dense plant communities with high vegetation cover, larger growth of individuals can be achieved as long as additional mineral nutrition and water are provided to sustain the increased growth (Watkinson 1983; Begon *et al.* 1996; Freckleton & Watkinson 2001; Craine & Dybzinski 2013). Asymmetric competition for light in such dense communities

shapes the structure of plant canopies (Nagashima & Hikosaka 2011) as well as the plant community as a whole (DeMalach *et al.* 2016). Plants that manage to survive under the shade of their taller neighbours can alter leaf morphology to adapt photosynthesis to reduced light availability (Valladares & Niinemets 2008). A common plastic response of individual plants is to increase the leaf area to leaf mass ratio (specific leaf area, SLA) to optimize light capture for growth maintenance (Milla & Reich 2007; Valladares & Niinemets 2008; Liu *et al.* 2016; Smart *et al.* 2017). Plants can also compete for light that is inherently scarce, such as in herbaceous communities on the forest floor that are shaded by large canopy trees (Valladares *et al.* 2016). Sudden gaps in the tree canopy enhance light availability and photosynthesis in the understorey at very short notice (Paul-Limoges *et al.* 2017). This change in available light can lead to rapid plastic responses in plant height and SLA (Valladares *et al.* 2002), in synchrony with shifts in community composition (De Frenne *et al.* 2015) and increased community biomass production (Jagodziński *et al.* 2016).

Apart from variation in light availability (Navas & Garnier 2002; Rozendaal *et al.* 2006; Lemke *et al.* 2015; Garnier *et al.* 2016; Burton *et al.* 2017), three main global change drivers are affecting temperate forest herb ecology (Gilliam, 2007) and thus potentially ITV. First, climate warming can alter growth and leaf trait values in herbaceous plants so that they come to resemble those of warm-adapted communities (Hoepfner & Dukes 2012; De Frenne *et al.* 2015; Helsen *et al.* 2017; Bjorkman *et al.* 2018; Henn *et al.* 2018). Second, nitrogen (N) deposition (Bobbink *et al.* 2010) can lead to increases in mean plant height and SLA by enhancing growth and increasing N content per unit dry mass of plant tissues (Hejman *et al.* 2012; Mao *et al.* 2017). Finally, elevated soil N and phosphorus (P) concentrations stemming from an agricultural land-use history can lead to increases in productivity and variability in functional leaf traits (Fraterrigo *et al.* 2009; Baeten *et al.* 2010, 2011; Siefert & Ritchie 2016). These drivers can interact to affect trait values in plant communities (Perring *et al.* 2016).

Plant functional traits can differ between species depending on how the species capture resources (Poorter *et al.* 2009; Garnier *et al.* 2016; Jagodziński *et al.* 2016; Mao *et al.* 2017). In forest herbs, there is evidence that life-history traits and plant height are correlated with forest colonization and specialization to forest habitat use (Verheyen *et al.* 2003). Herbaceous species that are confined to ancient forests are typically small in stature, slow colonizers that can photosynthesize in mature forests either as spring-flowering geophytes (Rothstein 2000; Tessier & Raynal 2003; Mabry *et al.* 2008) or as shade-tolerant species that can grow under fully developed tree canopies (Valladares & Niinemets 2008). These perennial ancient forest herbs consequently invest more nutrients into roots, bulbs, suckers or large seeds to allow proliferation (Verheyen *et al.* 2003), but at the cost of slow dispersal (Klimešová *et al.* 2016). In contrast, the ability of forest herbs to colonize post-agricultural forests correlates positively with large relative growth rates and rapid aging (Verheyen *et al.* 2003), both plant characteristics indicative of a 'fast life history' (Adler *et al.* 2014; Beckman *et al.* 2018). Such fast colonizers are tall and have light seeds that can be dispersed over longer distances than species typical of ancient forest (Verheyen *et al.* 2003; Thomson *et al.* 2011; Beckman *et al.* 2018). Fast colonizing forest herbs additionally have a high SLA and high leaf N content (Verheyen *et al.*

2003), leaf construction that favours resource acquisition over resource conservation (Wright *et al.* 2004; Adler *et al.* 2014; Reich 2014; Díaz *et al.* 2016). Fast colonizers could thus benefit more from variations in height and leaf traits than slow colonizers and could quickly capitalize on resources in rapidly changing environments (Alpert & Simms 2002).

Here we directly assess within-species responses of plant height and SLA to environmental change and land-use legacy, but also indirectly assess changes in vegetation cover. Furthermore, responses could also differ between species and these could potentially link to colonization capacity.

We performed a manipulative experiment with temperate herbaceous communities in forests comprising species with varying colonization capacities and affinities for forest habitat. This experiment will allow us to disentangle effects of enhanced light availability, warming, N addition and agricultural land-use history on intraspecific variation in plant height and SLA. We specifically hypothesize that:

- i within species, dense vegetation cover increases mean plant height and SLA, likely due to asymmetric competition for light. Higher vegetation cover could stem from community growth due to nutrient enrichment (from either N addition or an agricultural land-use history) or warmer and brighter conditions.
- ii within-species differences in mean plant height and SLA could result from variability in growing conditions induced by environmental changes and agricultural land-use history. The effects of these drivers can be interdependent. Specifically, we examine two-way interactions between enhanced light availability, warming, N addition and agricultural land-use history on changes in mean values for plant height and SLA.
- iii Species with good ability to colonize post-agricultural forests can exhibit more variability in trait values for both height and SLA. Since these species colonize novel environments, they need to cope with higher environmental unpredictability and could potentially benefit from larger trait variation than species confined to ancient forests.

MATERIAL AND METHODS

We performed a full-factorial experiment with 384 experimental units (mesocosms) to disentangle interactive two-level effects of forest agricultural land-use history, enhanced light availability, N addition and warming on 15 common European herbaceous forest species that differ in colonization capacity and affinity to forest habitat (Fig. 1). We measured plant height of 3445 individual plants and characterized SLA using 1125 measured leaf samples taken during the growing season of 2017, from the first week of March until the first week of September.

Land-use legacies: ancient and post-agricultural forest soils across environmental gradients

We collected soil (0.1 m³ in each forest) from eight temperate European regions across gradients of inherent soil fertility, regional P balance and N deposition (further details in Blondeel *et al.* 2019). Regions spanned from southwest Estonia (58°8' 45.10" N, 24°47' 04.83" E) to central France (47°50'



Fig. 1. Images of the multifactor experiment showing mesocosms in groups of four combined as a 'plot'. A: Overall view of the fenced area in the Aelmoeseneie forest (Belgium). B: A plot with a factorial combination of Warming and Light addition. C: Single treatment of Light addition, with a temperature sensor to measure air temperature. D: Control treatment where the plot is maintained by ambient conditions. Plots that receive the N enrichment treatment are not discernible in the field.

10.04° N, 2°45' 39.80° E) and included southern Sweden (55°32' 58.67° N, 13°14' 28.11° E), northwest Germany (53°20' 25.12° N, 9°25' 17.34° E), northeast Germany (53°13' 41.41° N, 12°07' 30.06° E), northern Belgium (51°00' 00.30° N, 4°20' 17.13° E), southern Belgium (50°03' 56.05° N, 4°22' 01.54° E) and northern France (49°53' 42.65° N, 2°18' 41.36° E). The collected soils were classified using cluster analysis into three groups according to inherent soil fertility (texture and calcareous properties). These soil types were either (i) 'eutrophic' – rich in clay and carbonates with high pH (6.6–7.1), (ii) 'oligotrophic' – high in sand with low pH (4.0–5.0) or (iii) 'mesotrophic' – intermediate fertility, siltier texture and intermediate pH (5.0–5.6) (see Blondeel *et al.* 2019). These soil groups are relative terms used to categorize inherent soil fertility within our samples and cannot be used for comparisons outside of our population. We use these categorical soil type variables as covariate when testing variation in mean plant height and mean SLA in response to interactive environmental changes (see section Data analysis).

To enable comparison by agricultural land-use history, we searched for three adjacent pairs of ancient or post-agricultural broadleaf forest with similar canopy composition within each region, leading to inclusion of 48 forest patches in the study (Blondeel *et al.* 2019). We searched for pairs of forest patches where one patch had been in existence pre-1850 (ancient forest) and the other had been established in the mid-20th century (post-agricultural forest). The agricultural legacies in the post-agricultural forest soils varied along gradients of inherent soil characteristics, regional P balance and N deposition (Blondeel *et al.* 2019). Overall, soils from post-agricultural forest had a higher pH ($+0.4 \pm 0.16$ (\pm SE), lower C:N (-1.49 ± 0.24), higher total P ($+118 \text{ mg}\cdot\text{kg}^{-1} \pm 60$) and higher Olsen P ($+13 \text{ mg}\cdot\text{kg}^{-1} \pm 5.5$) compared to ancient forest soils (Blondeel *et al.* 2019).

We collected a large volume of soil (ca. 0.1 m^3) in each forest patch from a pit with a depth of 15 cm and a surface area of $70 \times 100 \text{ cm}$. We transported all 48 collected soil samples to the long-term ecological research site (LTER) in the Aelmoeseneie forest in Belgium from November 2015 to February 2016

(50°58'30" N, 3°48'16" E, mean annual temperature (MAT) 10.6 °C, mean annual precipitation (MAP) 768 mm, 20 m a.s.l., N deposition (2016) $15.5 \text{ kg}\cdot\text{N}\cdot\text{ha}^{-1}$) (DEIMS-SDR Database, 2019). We sieved the 48 bulk soil samples through a 5-mm mesh sieve. The sampled soil from each forest patch was divided over eight mesocosms, one for each two-level factorial combination of light \times warming \times temperature. Each mesocosm consisted of 13-l sampled soil, placed in trays with 12 drainage holes ($46.5 \times 31.5 \text{ cm}$, depth 19.5 cm) on top of 9-l white sand to ensure good drainage. The bottom of the trays was first lined with root fabric to prevent plants from rooting into the underlying site soil when the mesocosms were buried; their upper edges were level with the surrounding ground.

Plant community assembly: slow and fast colonizers grown together

We compiled a pool of 15 species commonly found in temperate European forests (Table S1) and divided this species pool according to three emergent groups that are linked with a species' colonization capacity and affinity to forests habitat (Verheyen *et al.* 2003; De Frenne *et al.* 2011; Heinken *et al.* 2019). Verheyen *et al.* (2003) quantified differences in functional and life-history traits among 216 herbaceous species that colonize and establish in post-agricultural forests to varying degrees or remain confined to ancient forests, allowing the determination of traits that lead to successful colonization. The varying success between species in colonizing post-agricultural forest was captured in the colonization capacity index (CCI), where more negative values indicate a higher capacity to successfully colonize post-agricultural forests (Verheyen *et al.* 2003). The continuous CCI scale has values from -100 to $+100$, where -100 means that the species only occur in post-agricultural forest, while $+100$ means that the species are only found in ancient forest. The CCI scale thus allows estimation of a species' affinity to post-agricultural forest *versus* ancient forest. We classified these species in three groups based on our expert knowledge, guided by the CCI (Verheyen *et al.* 2003; De Frenne *et al.* 2011) and whether a species can be specified as a forest habitat specialist (Heinken *et al.* 2019). The first group (A) contained six poor colonizers and forest specialists, typical of ancient forest (Table S1). The second group (B) contained six intermediate colonizers of post-agricultural forest and not strict forest specialists (Table S1). The final group (C) contained three fast colonizing and generalist nitrophilic species with a higher affinity for post-agricultural forest and a large negative CCI (Table S1). We took both colonization of species and forest habitat specificity into account to classify these species. Hence, *Polygonatum multiflorum* is in group A as it is a typical forest species even though it has a relatively low CCI. Likewise, group B incorporates species with a wider range of habitat use that are not strict forest specialists. *Ajuga reptans* and *Poa nemoralis* can occur in grassy habitats and grasslands, while *Hedera helix* is often found in shaded urban and rural habitats. The groups supported the planting process (see below). We used the CCI directly to characterize each species in the analysis (see Data analysis) because of its established correlations between several life-history traits (Verheyen *et al.* 2003).

We created 12 species combinations (Table S2) in which we randomly assigned two poor colonizers (group A), two common colonizers of post-agricultural forest (group B) and one

fast-colonizing nitrophilic species (group C). These 12 species combinations serve as representative species assemblages in temperate mesotrophic deciduous forests in Europe and are solely used as random effect term in the analysis. The 12 species combinations were repeated four times over the 48 soil samples in each two-level factorial combination of light \times warming \times N addition (48 soil samples \times 8 factorial combinations = 384 mesocosms). We planted the 384 mesocosms in the first week of March 2016. Per mesocosm, we planted four individuals of each of the five species in a grid (7.0 \times 8.5 cm) in a randomized order using the *sample* function in R. This planting scheme results in 20 plants per mesocosm. The planted species were obtained from vegetative plant material (Table S1) and our plants were from either the local population in the Aelmoeseneie forest or Brakelbos (Belgium), or from a local plant nursery that supplies wild plants for horticulture (ECOFLOA, Halle, Belgium). During the first growing season (May, June, September 2016), we applied three rounds of weeding, where we eradicated species that had emerged spontaneously from the mesocosm soil. We buried all mesocosms with their top edges at surface level in a fenced area in the Aelmoeseneie Forest (Belgium) with a tree canopy (95% cover) dominated by *Fagus sylvatica*, *Quercus robur*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Larix decidua*. We buried mesocosms in 96 random groups ('Plots') of four mesocosms per plot to apply manipulative experimental treatments (see Fig. 1), as explained below, and following the methods of De Frenne *et al.* (2015). In total, we planted 7680 (384 mesocosms \times 20) individuals of 15 species (512 individuals per species).

Manipulating the environment: N addition, experimental warming and enhanced light availability

We applied three two-level environmental treatments in a full-factorial design from April 2016. Ongoing treatments consist of (i) N addition, (ii) experimental warming and (iii) enhanced light availability (Tables S3 and S4). The first treatment is N addition (further referred to as treatment 'N') by adding 0.25 l of a 2.01 g·l⁻¹ solution of NH₄NO₃ (50 kg·N·ha⁻¹·yr⁻¹·eq.) per mesocosm. We then rinsed the leaves with 0.25 l demineralized water to ensure that the applied N had not adhered to plant tissues. We performed this treatment four times per year at the start of each season, with the control mesocosms receiving 0.5 l demineralized water. The second treatment consisted of experimental warming (referred to as treatment 'T') in 75-cm diameter open-top chambers (OTC; De Frenne *et al.* 2010). We measured air temperature (15 cm above the forest floor), surface temperature (0 cm) and soil temperature (5 cm depth) in eight plots, one for each factorial combination of light \times warming \times N, using 24 thermocouples which log data every 30 s (Type T miniature; TC Direct, The Netherlands; datalogger type CR1000; Campbell Scientific, USA). In the first half of our sampling period (March 1 to May 31), the forest canopy was still developing, and light could easily reach the OTC in order to warm the chambers. During this period, we measured a significant increase ($P < 0.05$) in daily mean air temperature of 1.04 ± 0.47 °C, but no statistically significant increases in surface temperature (0.46 ± 0.26 °C) or soil temperature (0.13 ± 0.30 °C) at 5 cm depth (Figure S1). In the latter half of our sampling period (June 1 to August 31), the forest canopy was closed, which resulted in less effective

warming, but no significant differences ($P > 0.05$) between the warming and control treatments at any depth. The third treatment, light addition (referred to as 'L'), added 23.98 ± 4.40 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR to the ambient light (7.79 ± 0.68 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ under fully closed canopy) using two 18 W fluorescent tubes suspended 75 cm above ground level in each plot (Figure S2). This increment in light availability is equivalent to a small forest gap, and could lead to a three-fold increase in C assimilation rates in typical forest understorey plants (Rothstein & Zak 2001). The lamps were programmed to follow the natural photoperiod throughout the year and did not significantly affect air temperature (De Frenne *et al.* 2015). Control plots received ambient light and included a dummy lamppost suspended over the plot to account for any side effects of the lamp installation other than light addition (e.g. precipitation, interception; see Fig. 1).

Plant trait and community measurements

We measured plant height and SLA in the second growing season of the experiment, from March 2017 to September 2017, at the time of each species estimated peak biomass (Table S1). We chose not to measure reproductive traits (*i.e.* seed mass), as proposed in the leaf–height–seed scheme (Westoby 1998; Laughlin *et al.* 2010). Seed mass and plant height are strongly positively correlated in the global plant trait spectrum (Thomson *et al.* 2011; Díaz *et al.* 2016; Beckman *et al.* 2018), but also in forest herb species (Verheyen *et al.* 2003). Furthermore, several herbaceous species in our pool are clonal, with limited seeding (Klimešová *et al.* 2016). Moreover, these reproductive traits would have required more intensive measurement, given our large numbers of test plants (Pérez-Harguindeguy *et al.* 2013).

We measured plant height on 3445 survivors of the 7680 initially planted individuals (45% survival). The number of height measurements (*i.e.* individual survivors) did not depend on treatment effects (Figure S3); there were differences in survival among species (Tables S1 and S5). Vegetative plant height was measured as the shortest distance between ground level and the upper boundary of the main photosynthetic tissues; *i.e.* we only measured foliage height, not inflorescence or seeding height (Pérez-Harguindeguy *et al.* 2013). We measured plant height in centimetres to one decimal place using a common folding meter rule.

We measured average SLA as the one-sided area of multiple leaves from a single species in each mesocosm, divided by the oven-dry mass and expressed as $\text{mm}^2\cdot\text{mg}^{-1}$ (Pérez-Harguindeguy *et al.* 2013). We collected up to eight healthy leaves of each species and no more than two per individual to avoid excessive damage to any individual plant. We only sampled outer leaves (excluding petioles) because SLA can be strongly affected by light intensity (Pérez-Harguindeguy *et al.* 2013). The amount of SLA measurements did not vary due to treatments within any species (Figure S4), while there were larger differences in measured SLA between species (Tables S1 and S5). The projected area of the leaves was measured with the *Easy leaf area* free mobile phone application (Easlon & Bloom 2014) within 2 h of picking the leaves, after taking a photograph with a mobile phone (13 MP camera). This open-source software package can estimate green leaf area in a R-G-B photograph by counting the total number of green pixels and

converting this into an area measurement by counting red pixels from a 4 cm² calibration square provided in the image. After the area measurement (mm²), each leaf sample was dried in an oven at 65 °C for 48 h to constant mass (in mg).

We measured total vegetation cover (%), which is tightly linked to productivity, leaf biomass and competition for light (Muukkonen *et al.* 2006). We measured vegetation cover as the one-sided projection of vegetation in each tray. This was measured twice during the experiment: 4 May and 11 August. We used digital R-G-B photographs of the mesocosms taken perpendicular to the ground, and used the *Canopy Area* tool to measure green pixels of vegetation and recalculate this as percentage cover (Easlon & Bloom 2014).

Data analysis

All data analysis was performed in R (R Core Team 2019). We performed three analyses to assess whether trait variation in plant height and SLA within a species is a function of (1) vegetation cover, (2) agricultural land-use history interacting with multiple environmental drivers, and (3) species colonization ability. We consequently addressed within-species trait variation in two ways. First, by assessing change in mean trait values due to vegetation cover and treatment (hypotheses (1) and (2), respectively). Second, by examining variability in traits across all measured values *via* the coefficient of variation (CV; hypothesis (3)). Prior to analyses, we excluded *Glechoma hederacea* because there were <30 measurements available (see Table S1). During analyses on variations in mean height and SLA (hypotheses (1) and (2)), *Geranium robertianum* was excluded because there were too few measurements to robustly fit the model structure.

In the first analysis, we tested whether vegetation cover explains differences in mean plant height and SLA in each species (hypothesis 1). We calculated separate hierarchical linear mixed-effects models (package: nlme, Pinheiro *et al.* 2019) for each species to estimate the mean trait value in response to vegetation cover. The original Region of the soil (8 levels), Community (12 levels) and Plot (96 levels) are separate random effect terms in this structure, *i.e.* (1|Region) + (1|Community) + (1|Plot). Adding the 'Plot' random effect term was not possible for SLA because of limited degrees of freedom (SLA is an averaged measure for each species in each mesocosm). The predictor variable is the average vegetation cover (%) of each mesocosm measured between May 2017 and August 2017. We checked normality in residuals with a Shapiro-Wilk test (function shapiro.test with the stats package) on each model, and log-transformed the response variable when necessary to achieve normality in model residuals. Log transformation of the response was needed for six species in plant height and five species in SLA (see Table S6). We additionally tested whether the covariate (Soil type) and two-way interactions (including main effects) of agricultural land-use history (LU), enhanced light availability (L), nitrogen addition (N) and warming (T) directly explained variation in total vegetation cover. We used the same hierarchical model structure as explained above.

We tested hypothesis (2) by estimating mean plant height and SLA of species in response to two-way interactions of agricultural land-use history (LU), enhanced light availability (L), N addition (N) and warming (T). We calculated separate hierarchical linear mixed-effects models (function lme in package

nlme; Perring *et al.* 2018a,b) for each species with six double interactions including all four main effects (LU, L, N, T, LU:L, LU:N, LU:T, L:N, L:T, N:T) and an extra covariate 'Soil type'. We included the covariate Soil type (three levels: eutrophic, mesotrophic, oligotrophic) in the models because inherent soil fertility can be a major source of trait variation, even though it is not one of our focal environmental change predictors. The random effects structure of these models is the same as in hypothesis (1), with 'Region' (8 levels), 'Community combination' (12 levels) and 'Plot' (96 levels) included. Prior to computing, we checked normality assumptions using a Shapiro-Wilk test (function shapiro.test in stats package) for each model accompanied with a qq-plot and histogram of model residuals. Data were log-transformed when necessary to achieve normality of residuals, which was the case for seven species for plant height and six species for SLA (see Table S7). We performed ANOVA (*F*-test, function anova in stats package) on one linear model for each of the 13 species per trait, which contains 11 terms per model (four main effects, six double interactions, one covariate main effect). We applied an adjusted alpha ($P < 0.007$) so that the expected value of a false positive effect is <1 out of the 143 tested terms ($\alpha = 1/143 = 0.007$) for a given trait. If we had used the common alpha of $P < 0.05$, the expected value of interpreting false positive effects would have been seven terms ($143 \times 0.05 = 7.15$) for each trait.

We tested hypothesis (3) by calculating the CV for each species across all measurements of height and SLA. We performed linear regression of the CV as function of species capacity to colonize post-agricultural forest. We used the colonization capacity index (CCI) to determine species ability to successfully colonize post-agricultural forest (Verheyen *et al.* 2003), where more negative values denote a larger colonization capacity. We calculated the CV for plant height and SLA for the whole range of species trait values (across all treatments) as the ratio of standard deviation to estimate of population mean. The CV is a simple measure of general intraspecific trait variation and phenotypic plasticity, *i.e.* when traits are not measured on individuals of the same genotype but of the same species (Valdareo *et al.* 2006). As we computed one CV for each species for the whole dataset, we performed a non-hierarchical linear regression (function lm in stats package) of species CV in response to the species CCI for both traits ($\alpha = 0.05$).

RESULTS

Response of mean traits to vegetation cover

In the first analysis, we found that increasing vegetation cover was related to changes in mean values of both height and SLA. Vegetation cover (Table 1) was significantly higher on post-agricultural forest soils ($+6.06 \pm 1.68$), with light addition ($+15.88 \pm 1.79$) and with warming ($+8.41 \pm 1.83$). There was no evidence for interactions between environmental treatments in vegetation cover. In turn, vegetation cover affected both species mean height and mean SLA, while mean height was more responsive to vegetation cover than mean SLA (Fig. 2). Ten of the 13 species had increasing mean height estimates with increasing vegetation cover, all $P < 0.001$ (Table S6). The largest absolute increase in height was in *Urtica dioica*, which was also the fastest colonizer into post-agricultural forest (most negative CCI), with predicted mean height 15.8 cm (95% CI:

Table 1. Model fit of the significant ($P < 0.05$) treatments that influenced mean vegetation cover (%)

Term	Estimate	\pm SE	df	F-value	P-value
Intercept	43.15	3.40	276	376	<0.0001
Post-agricultural	+6.06	1.68	9	12	0.0074
Light addition	+15.88	1.79	276	79	<0.0001
Warming	+8.41	1.83	276	21	<0.0001

Estimates \pm SE, denominator df, F-value and P-value are given for model terms. The three fixed effect terms were two-level terms: land-use history (LU), light treatment (L) and temperature treatment (T) which together explained <20% of variation ($R^2_m = 0.17$); 65% of variation is accounted for when including the random effect terms (R^2_c) i.e. Region of soil, Plot and community combination. The intercept term is average intercept across random effect terms and is the estimate for an ancient forest soil with control treatments for light and warming.

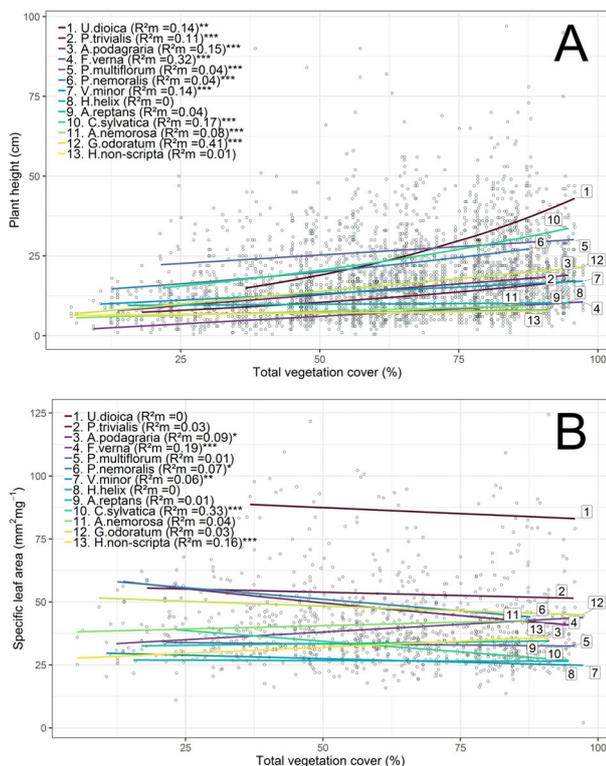


Fig. 2. Plant height (A) is more responsive to total vegetation cover than SLA (B) across species. Results of within species linear mixed-effects models testing plant height and SLA in response to total vegetation cover in a mesocosm. Significance: 0.05*, 0.01** and 0.001***. The lines are average predicted values of linear mixed-effects model for each species (either normal or log-transformed response). Marginal R^2 (R^2_m) values are given, which denote model fit on the only fixed effect (vegetation cover). Species are ordered on colonization capacity index (CCI), with the fastest colonizers into post-agricultural forest at the top left and colours purple–blue–yellow representing fast to slow colonizers.

8.4–29.7 cm) at the lowest CCI (36%) and 41.6 cm (95% CI: 22.2–78.0 cm) at the highest CCI (96%); i.e. over the range of total cover values in which it occurred, a relative increase in mean height of 160%. However, the largest relative increase

was five-fold mean height in *Ficaria verna*; this species increased its mean height from 1.9 cm (95% CI: 1.05–2.83 cm) at 9% total cover to 10.6 cm (95% CI: 8.7–12.5 cm) at a vegetation cover of 97%.

For SLA, we found both significant increases and decreases in response to community vegetation cover, depending on species. Species mean SLA decreased significantly in four species (*Aegopodium podagraria*, *Poa nemoralis*, *Vinca minor*, *Carex sylvatica*) and increased in two (*Ficaria verna*, *Hyacinthoides non-scripta*) in response to vegetation cover. However, the slopes were not as pronounced as for the height response (Fig. 2), with a 30% maximum decrease of SLA for both *A. podagraria* and *C. sylvatica*. The significant increases were of similar magnitude: 31% for *F. verna* and 30% for *H. non-scripta* (Table S6).

Response of mean traits to environmental treatments

Plant height increased in response to environmental treatments and agricultural land-use history across several species ($P < 0.007$, see Table S7 for P-values). The pattern in significant responses (Fig. 3) shows that six species had significant height responses (excluding the Soil type covariate), mostly in slow-colonizing species (5 species) compared to fast-colonizing species (1 species). However, the covariate ‘Soil type’ significantly affected height in three species, all relatively fast colonizers based on CCI. The most important significant ($P < 0.007$) main effect on the height response was light addition, which increased height for four species (Fig. 4A; Table S8). The largest relative increase in mean height in response to light was in *U. dioica* (+65%) followed by *C. sylvatica* (+40%), *Anemone*

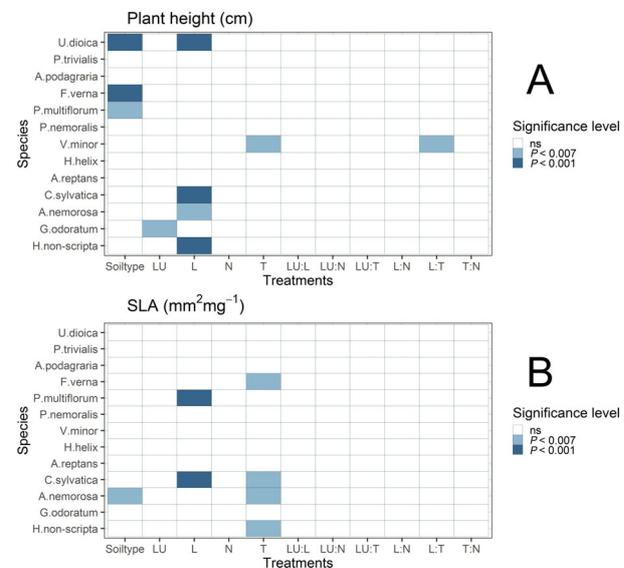
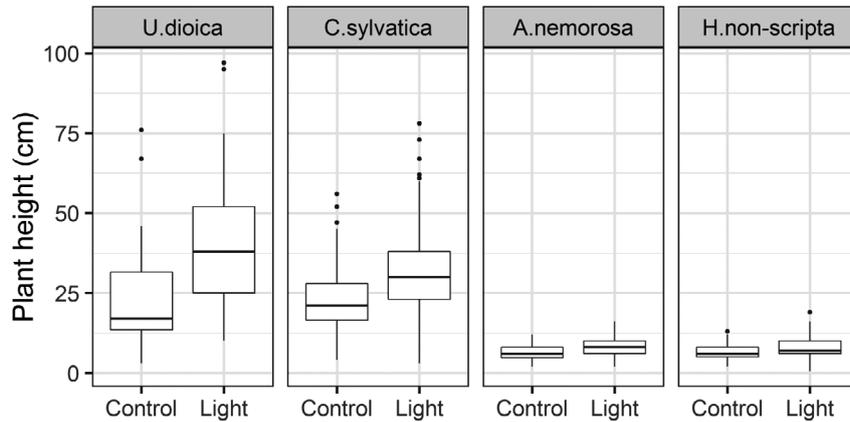


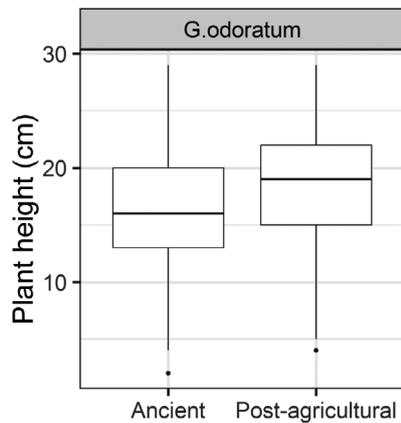
Fig. 3. Species selectively respond to environmental change through both plant height (A) and specific leaf area (SLA) (B). Results of ANOVA ($P < 0.007$) for two-way interactions of the forest’s land-use history (LU), light availability (L), nitrogen addition (N) and warming (T). We applied an adjusted alpha ($P < 0.007$) so that the expected value of a false positive effect is <1 out of the 143 tested terms ($\alpha = 1/143 = 0.007$). Species are ordered on colonization capacity index (CCI), with the fastest colonizers into post-agricultural forest at the top.

Significant Plant height effects

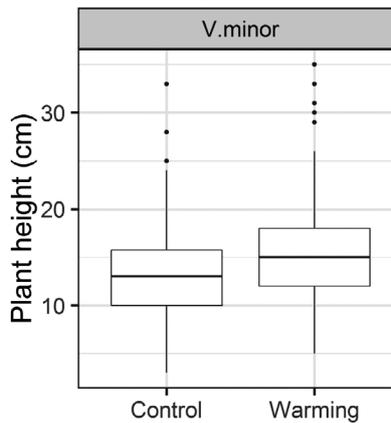
A. Light addition (L)



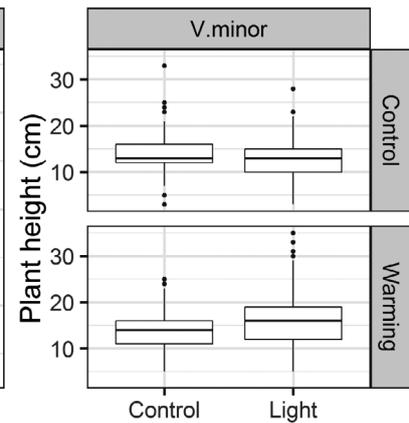
B. Land-use History (LU)



C. Warming (T)

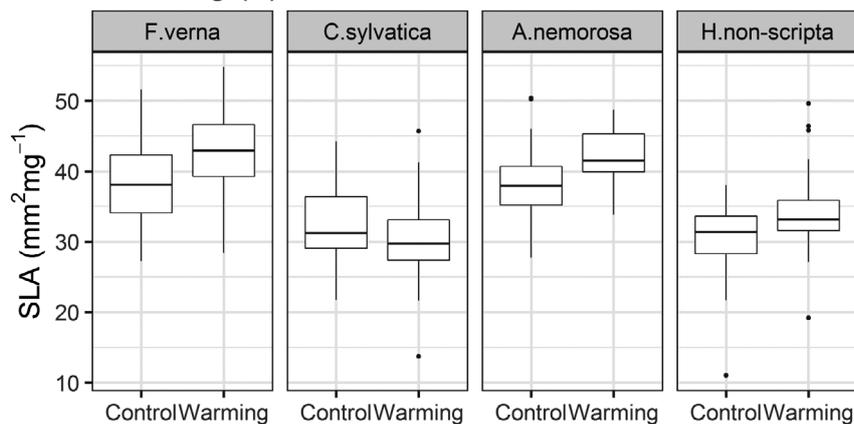


D. Interaction of L*T



Significant SLA effects

E. Warming (T)



F. Light addition (L)

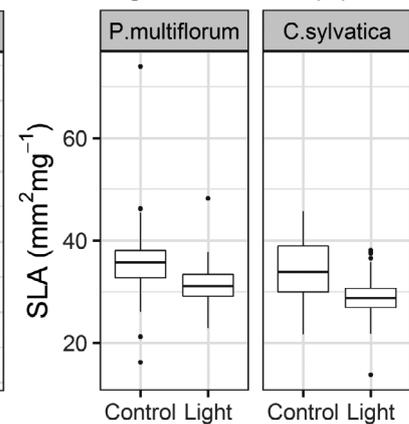


Fig. 4. Significant effects ($P < 0.007$) of experimental treatments on within-species plant height (A–D) and SLA (E, F). Panels illustrate significant effects shown in Fig. 3. Species are ordered on colonization capacity index (CCI) with faster colonizers into post-agricultural forest on the left.

nemorosa (+28%) and *H. non-scripta* (+19%). Nitrogen addition did not affect any species. Agricultural land-use history and warming affected mean height of one species, *Galium*

odoratum responded positively to agricultural land-use history, with a relative increase in mean height of 15% (Fig. 4B; Table S8). *Vinca minor* responded positively to warming as a

main effect with a relative increase of 2% (Fig. 4C; Table S8); however, the warming effect depended on light addition and, when added together, height increased by 33%. This was the only interaction found in the analysis across all considered species (Fig. 4D; Table S8).

Specific leaf area (SLA) was less significant than height for the environmental treatments and agricultural land-use history (Fig. 3). The most common significant ($P < 0.007$) main effect was warming, which increased SLA 11% for *H. non-scripta*, 9% for *A. nemorosa* and 10% for *F. verna*. Warming negatively affected SLA of *C. sylvatica*, with a decrease of 6% (Fig. 4E; Table S8). Light addition had a significant negative main effect on two species: *C. sylvatica* (15% decrease) and *Polygonatum multiflorum* (10% decrease) (Fig. 4F; Table S8). The SLA within species did not respond to N addition or forest land-use history and there were no significant interactions. In summary, SLA increased in response to warming in the early-flowering species *H. non-scripta*, *A. nemorosa* and *F. verna*; conversely, SLA decreased in late-flowering species in response to both light and warming (separately) for *C. sylvatica*.

Intraspecific trait variation in relation to a species colonization capacity

In the final analysis (Fig. 5), the CV for plant height was highest ($P = 0.001$, $R^2 = 0.61$) for fast-colonizing species into post-agricultural forest (negative CCI). The CV for height ranged from 0.29 for the slow-colonizing *G. odoratum* to 0.71 for the fast-colonizing *P. trivialis*. The CV for SLA ranged from 0.12 for slow-colonizing *A. nemorosa* to 0.33 for the fast-colonizing *Aegopodium podagraria*, but this response of SLA to species CCI was not statistically significant ($P = 0.50$, $R^2 = 0.038$). Fast colonizers into post-agricultural forest thus showed more intraspecific variation in height as measured by CV than slow colonizers across the whole trait range, but not for SLA.

DISCUSSION

We found that variation in plant height and SLA of forest herbs under the environmental changes were related to the function of the trait. Generally, trait values of most species did not respond to more than one main effect of a treatment. Interactions between multiple environmental treatments were rarely

important in explaining variation in mean trait values of species. However, there were generalizable patterns in plant height and SLA response across species. Mean height values increased as vegetation cover increased in response to light addition, warming and agricultural land-use history. The CV for height was larger in fast-colonizing species. In contrast, changes in mean SLA only occurred within selected species to improve light acquisition in shaded conditions. These individualistic, functional trait responses to a single factor benefit growth of a specific species in the short term (Garnier *et al.* 2016). Our results suggest that (i) variation in height is related to increased vegetation cover in brighter conditions and largely benefits fast colonizers, and (ii) changing SLA is beneficial for species that have acclimatized to shaded conditions in forests, *i.e.* vernal geophytes and shade-tolerant species.

Intraspecific variation in plant height

The variability in mean plant height could benefit growth, light acquisition and dispersal (Moles *et al.* 2009). Plant size differences between individuals in communities can be an outcome of asymmetric competition for light (DeMalach *et al.* 2016), as individuals invest in height to disproportionately capture light from neighbours when vegetation becomes dense (Freckleton & Watkinson 2001). We observed that mean vegetation cover of the community increased from 40% to 75% primarily due to combined effects of light addition, followed by warming and an agricultural land-use history. As the vegetation became denser and increased to maximum cover, individuals of ten of the 13 species nearly doubled in mean height. This height response to vegetation cover was stronger than the height response of species to direct environmental change. This could indicate that competition mediated by larger vegetation cover better explains height change than altered environmental conditions *per se*. A large meta-analysis of functional trait variation in forest herbs also found that changing vegetation cover, through environmental changes or other factors, was a strong predictor of larger height values in forest herbs (Burton *et al.* 2017).

Light was the main driver for mean height increases, affecting four out of 13 species. Lemke *et al.* (2015) also found that height increased in response to light availability, but only in a graminoid and not in a forb species. Warming was of minor importance and affected one out of 13 species. We had

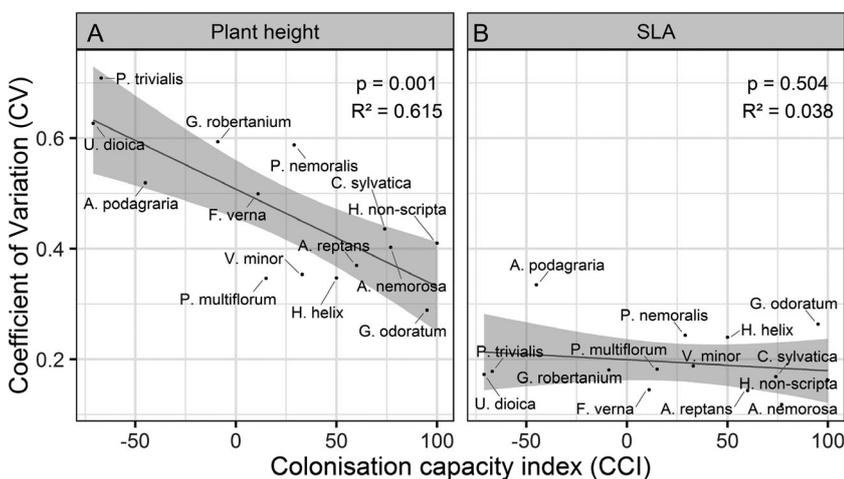


Fig. 5. Faster colonizers into post-agricultural forest have significantly higher intraspecific trait variation (ITV) for plant height (A) but not SLA (B). Coefficient of variation (CV) for plant height (A) and SLA (B) for each species in regression (95% CI) to that species' colonization capacity index (CCI). CCI values closer to 100 indicate higher affinity for ancient forest; values closer to -100 indicate faster colonization into post-agricultural forest (Verheyen *et al.* 2003).

expected that more species would respond positively to warming, given that individuals of forest herb species are taller in warmer areas of their range (Kollmann & Bañuelos 2004; De Frenne *et al.* 2011; De Frenne *et al.* 2014; Lemke *et al.* 2015). Agricultural land-use history and N addition had hardly any effect on plant height. This suggests that, in general, nutrient availability was less limiting than light availability. Adding ca. 50 kg-N·ha⁻¹·year⁻¹ (equivalent of N deposition near a point source, e.g. a pig farm) had limited individual responses. This is likely due to high ambient N deposition (15.5 kg-N·ha⁻¹·year⁻¹), which is within the critical load (10–20 kg-N·ha⁻¹·year⁻¹) for temperate broadleaf forest (Bobbink *et al.* 2015). However, including inherent soil fertility as a covariate in the analysis did explain mean plant height differences in three species. This suggests that the influence of pH on nutrient availability might also be an important driver of trait variation (Siefert 2012). Other studies suggest that nutrient enrichment through N addition or agricultural land-use history can increase height of some forest herbs, resulting in a taller plant community (Baeten *et al.* 2010; Tatarko & Knops 2018). However, many of these studies were performed on individual species in pots, rather than in a field community, such as used in our study. The relatively low number of responses in height to direct environmental change could thus suggest that community properties (*i.e.* vegetation cover) determine an individual's short-term response to environmental change (Bennett *et al.* 2016).

We also found that variability in height (CV) was larger in species with good colonization capacity into post-agricultural forest than in slow colonizers. For fast-colonizing wind-dispersed species, plasticity in height is important to disperse seed further from neighbouring plants (Thomson *et al.* 2011), apart from the benefit in capturing light (Freckleton & Watkinson 2001). Slow-colonizing forest herbs need to invest less resources in aboveground biomass to disperse, as bud banks are more common in such species and facilitate multiplication (Klimešová *et al.* 2016; Ott *et al.* 2019). Overall, these findings suggest that variation in plant height largely benefits fast colonizers when vegetation cover is high.

Intraspecific variation in SLA

Specific leaf area is a functional trait related to trade-offs in photosynthetic capacity and the associated leaf economics spectrum (Wright *et al.* 2004). We observed responses in SLA in species typical of shaded temperate forests but did not find a clear relationship between colonization capacity and the CV of SLA in a species. SLA responded only to light and warming, and only in shade-avoiding geophytes or shade-tolerant plants that grow under a closed canopy (Verheyen *et al.* 2003; De Frenne *et al.* 2011). Interestingly, within-species SLA can both increase and decrease in response to a gradient from shady to sunny conditions (Garnier *et al.* 2016), as observed in our study for contrasting responses to warming and light addition.

Growth temperatures can positively affect SLA of individual species (Atkin *et al.* 2006) and for forest herbs along latitudinal (De Frenne *et al.* 2011) and elevation (Midolo *et al.* 2019) gradients, where lower SLA is expected at colder, higher latitudes and altitudes. The increasing mean SLA in response to warming of the early-flowering geophytes *H. non-scripta*, *A. nemorosa* and *F. verna* would thus be advantageous for such

spring-flowering geophytes. These are the three earliest species in our species pool to reach peak biomass and must withstand frost in early spring while sustaining growth. A common response to low air temperatures is to produce thicker leaves, which raises leaf biomass (Pérez-Harguindeguy *et al.* 2013) but requires an important mass–investment trade-off, considering the short lifespan of the leaves (Wright *et al.* 2004; Jagodziński *et al.* 2016). The above three vernal species likely benefitted from the 1 °C increase in air temperature because they had decreases in leaf thickness and thus mass investment, leading to a higher photosynthetic surface area per unit mass investment (SLA). Conversely, SLA decreased in response to light in *C. sylvatica* and *P. multiflorum*, which are shade-tolerant species that can flower under closed canopies in ancient forests (Wulf 1997; Bossuyt *et al.* 1999). Shade-tolerant species do not generally have plastic leaf physiology, but can change leaf morphology (Wright *et al.* 2004; Milla & Reich 2007; Valladares & Niinemets 2008). Individual plants usually develop a higher SLA when grown under low light conditions (Reich *et al.* 2003; Rozendaal *et al.* 2006; Feng & Van Kleunen 2014; Liu *et al.* 2016) to optimize light capture and carbon gain in such environments (Evans & Poorter 2001). A lower SLA found in the shade-tolerant species *C. sylvatica* and *P. multiflorum* in the light treatment followed this pattern.

There were limited effects of N addition and agricultural land-use history on SLA of the studied species. Other studies suggest that intraspecific SLA has either a limited or positive response to enhanced nutrient availability in response to agricultural land-use history (Siefert 2012; Siefert & Ritchie 2016) or N addition (Zhou *et al.* 2018; Firn *et al.* 2019). However, leaf nutrient content and leaf dry matter are more consistent in predicting leaf trait variation in response to increased nutrient availability (Smart *et al.* 2017; Firn *et al.* 2019). The SLA of many forest herbs is sensitive to changing light availability, therefore SLA is not a reliable predictor of altered nutrient availability (Burton *et al.* 2017).

Perspectives on trait variation in a changing world

Our experimental design allowed us to disentangle the effects of several environmental change treatments on trait expression of typical forest herb species. A major outcome of this experiment is the lack of treatment interactions on ITV. Instead, simple univariate treatment responses of height and SLA were detected. Patterns in plant species growth responses to warming (Hollister *et al.* 2005), light availability (Rozendaal *et al.* 2006) and increased nutrient availability (Fynn & O'Connor 2005) have long been shown to be dependent on the species studied, suggesting different limiting factors for species that naturally occur within the same community (Chapin & Shaver 1985). Such selective plant responses to our changes in environmental factors imply a 'Gleasonian' perspective regarding plant responses to global change and consequent effects on community organization: where trait expression of individual species to changes in simple environmental factors determines the interactions between species within the community (Gleason 1926; Nicolson & Mcintosh 2002; Götzenberger *et al.* 2012). This could, however, be a gross underestimate of the complex multidimensional interactions between energy and nutrients, consumers and competitors, and time in affecting plasticity of traits in examined communities (Westneat *et al.*

2019). Our experimental approach did allow us to reveal the importance of individual drivers that interact in the natural world. Important factors include light availability and warming in forest gap conditions, and species composition of understorey communities in relation to agricultural land-use history. This disentangled view showed that vegetation cover did respond to environmental changes and such changes affected trait values of the species. Individual species responses further promoted ITV in response to changing resources and conditions.

Apart from competition within the community affecting ITV (Bennett *et al.* 2016), species richness effects on ITV could also occur as a result of resource partitioning (Lipowsky *et al.* 2015). We did not examine these effects by keeping constant species richness across communities at the time of planting (five species) so as not to inflate the experimental design. We also did not examine genetic variation within species, as this component and local adaptation in ITV generally become more prominent at larger geographic scales (Albert *et al.* 2011; Lajoie & Vellend 2015; Moran *et al.* 2016; Veresoglou & Penuelas 2019). However, it is likely that local adaptation of species across a large geographic gradient could alter trade-offs between functional traits within species (Oldfather 2019). Such genetic variation between populations could consequently influence the magnitude of ITV in response to environmental change (Kahl *et al.* 2019).

Contrary to our expectations, this short-term mesocosm experiment barely revealed any interactive effects between the multiple treatments on plant trait variation. This lack of interaction in the short term does not imply that such interactive effects are not important for functional trait responses to global change. Rather it shows the complementarity of experimental research to long-term vegetation resurveys (Verstraeten *et al.* 2013; Perring *et al.* 2018; Perring *et al.* 2018) or mechanistic modelling approaches (Dirnböck *et al.* 2017; Landuyt *et al.* 2018). Long-term experiments, vegetation resurveys and modelling are perhaps better suited to unravel such long-term interactive effects between global change drivers of understorey trait variation (Luo *et al.* 2011; Verheyen *et al.* 2017). Most probably, interactions between the treatments in this experiment could emerge after a longer time, when resources and conditions other than light become more limiting (Oliver & Morecroft 2014).

Conclusions and future directions

Estimating ITV in response to land-use legacies (Siefert & Ritchie 2016) and environmental changes (Bolnick *et al.* 2011; Albert *et al.* 2011) are important for predicting the future of plant communities. Here we assessed ITV in plant height and SLA of forest herbs with different colonization abilities and affinities to forest habitat in terms of community growth and multiple environmental changes, at a local scale *via* a manipulation experiment. Contrary to our expectations, we found that interactions between environmental drivers were not important in explaining variation in traits. A lack of interactive treatment effects could suggest that traits respond at an individual species level to single factors that benefit the species growth. We showed that increases in within-species mean height relate to higher vegetation cover in higher available light conditions, which largely benefitted rapid colonizers. Trait variation in SLA promoted species that are acclimated to the shade conditions of forests, as within-species mean SLA distinguished

between shade-avoiding vernal species that responded to warming and shade-tolerant species that responded to light addition.

The responses in plant height and SLA occurred after one growing season following herb layer establishment of the experimental communities. At this time point, understorey plant responses to environmental change remained individualistic, but over decades after the initial trait response (Gross *et al.* 2009) these patterns might reveal changes in community assembly towards fast-growing and fast-colonizing species in disturbed forests when light availability is high. When typical forest herbs are introduced into such disturbed forests, these could be excluded from community assembly in the long term by establishment of more generalist species (see Baeten & Verheyen 2017). Patterns in ITV at initial stages of plant species establishment could thus potentially reflect the trajectory in community assembly after prolonged time periods.

AUTHOR CONTRIBUTIONS

HB, PDF, EDL, LD, SLM, MPP and KV designed the study. SG and PV added conceptual views in a later stage of the study. HB and EDL collected the data. HB performed statistical analyses, with significant inputs from MPP, DL and KV. HB led writing of the manuscript, with significant inputs from MPP and KV. All authors provided comments on the manuscript at several stages during its development.

DATA ARCHIVING

Data will be made available via <http://www.pastforward.ugent.be/data.html>

FUNDING INFORMATION

This work was supported by the European Research Council (ERC) through PASTFORWARD [ERC Consolidator Grant 614839, assigned to KV]. We thank the Research Foundation – Flanders (FWO) for supporting DL.

ACKNOWLEDGEMENTS

Special thanks to Laurent Bergès, Jörg Brunet, Guillaume Decocq, Martin Diekmann, Jaan Liira and Monika Wulf for help with relocation of the forest patches for the soil collection. We thank Filip Ceunen, Kris Ceunen and Luc Willems for technical support in setting up the experiment. We thank all 30+ colleagues in the Forest & Nature Lab who helped with planting and mesocosm establishment in March 2016. We thank all people who helped in collecting trait data: Adrien Berquer, Kris Ceunen and Robbe De Beelde. We thank the reviewers and editor for providing valuable comments on the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Pool of 15 species used in the experiment and their most important attributes. Scientific names are from the

plantlist.org. Number of measurements (No.) for height (maximum 512) and SLA (maximum 128) are given.

Table S2. Species combinations in the twelve communities.

Table S3. Estimates of temperature measurements (°C).

Table S4. All 384 mesocosms and their most important characteristics.

Table S5. Number of measurements within each combination of temperature (T), Light addition (L), N addition (N) and the land-use history of the soil (Ancient *versus* Post-agricultural).

Table S6. Coefficients of the models with total vegetation cover (%) as a predictor, with plant height in cm and SLA in $\text{mm}^2 \cdot \text{mg}^{-1}$.

Table S7. All ANOVA results (143 terms per trait from 13 species), of the model with structure Soiltype + LU*L + LU*T + LU*N + L*T + L*N + T*N + (1|COM) + (1|Region) + (1|Plot).

REFERENCES

- Adler P.B., Salguero-Gomez R., Compagnoni A., Hsu J.S., Ray-Mukherjee J., Mbeau-Ache C., Franco M. (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 740–745.
- Albert C.H., Thuiller W., Yoccoz N.G., Soudant A., Boucher F., Saccone P., Lavorel S. (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, **98**, 604–613.
- Albert C.H., Grassein F., Schurr F.M., Vieilledent G., Violle C. (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 217–225.
- Alpert P., Simms E.L. (2002) The relative advantages of plasticity and fixity in different environments: when is it good for a plant to adjust? *Evolutionary Ecology*, **16**, 285–297.
- Atkin O.K., Loveys B.R., Atkinson L.J., Pons T.L. (2006) Phenotypic plasticity and growth temperature: understanding interspecific variability. *Journal of Experimental Botany*, **57**, 267–281.
- Baeten L., Verheyen K. (2017) Changes in the nature of environmental limitation in two forest herbs during two decades of forest succession. *Journal of Vegetation Science*, **28**, 883–892.
- Baeten L., Vanhellefont M., De Frenne P., De Schrijver A., Hermy M., Verheyen K. (2010) Plasticity in response to phosphorus and light availability in four forest herbs. *Oecologia*, **163**, 1021–1032.
- Baeten L., Verstraeten G., De Frenne P., Vanhellefont M., Wuyts K., Hermy M., Verheyen K. (2011) Former land use affects the nitrogen and phosphorus concentrations and biomass of forest herbs. *Plant Ecology*, **212**, 901–909.
- Beckman N.G., Bullock J.M., Salguero-Gómez R. (2018) High dispersal ability is related to fast life-history strategies. *Journal of Ecology*, **106**, 1349–1362.
- Begon M., Harper J.L., Townsend C.R. (1996) *Ecology: individuals, populations and communities*. 3rd edn. Blackwell Science, Chichester UK.
- Bennett J.A., Riibak K., Tamme R., Lewis R.J., Pärtel M. (2016) The reciprocal relationship between competition and intraspecific trait variation (M. Semchenko, Ed.). *Journal of Ecology*, **104**, 1410–1420.
- Bjorkman A.D., Myers-Smith I.H., Elmendorf S.C., Normand S., Rüger N., Beck P.S.A., Blach-Overgaard A., Blok D., Cornelissen J.H.C., Forbes B.C., Georges D., Goetz S.J., Guay K.C., Henry G.H.R., HilleRisLambers J., Hollister R.D., Karger D.N., Kattge J., Manning P., Prevéy J.S., Rixen C., Schaepman-Strub G., Thomas H.J.D., Vellend M., Wilms M., Wipf S., Carbone M., Hermandutz L., Lévesque E., Molau U., Petraglia A., Soudzilovskaia N.A., Spasojevic M.J., Tomaselli M., Vowles T., Alatalo J.M., Alexander H.D., Anadon-Rosell A., Angers-Blondin S., Beest M.T., Berner L., Björk R.G., Buchwal A., Buras A., Christie K., Cooper E.J., Dullinger S., Elberling B., Eskelinen A., Frei E.R., Grau O., Grogan P., Hallinger M., Harper K.A., Heijmans M.M.P.D., Hudson J., Hülber K., Iturrate-García M., Iversen C.M., Jaroszynska F., Johnstone J.F., Jørgensen R.H., Kaarlejärvi E., Klady R., Kuleza S., Kulonen A., Lamarque L.J., Lantz T., Little C.J., Speed J.D.M., Michelsen A., Milbau A., Nabe-Nielsen J., Nielsen S.S., Ninot J.M., Oberbauer S.F., Olofsson J., Onipchenko V.G., Rumpf S.B., Semchenko P., Shetti R., Collier L.S., Street L.E., Suding K.N., Tape K.D., Trant A., Treier U.A., Tremblay J.-P., Tremblay M., Venn S., Weijers S., Zamin T., Boulanger-Lapointe N., Gould W.A., Hik D.S., Hofgaard A., Jónsdóttir I.S., Jørgensen J., Klein J., Magnusson B., Tweedie C., Wookey P.A., Bahn M., Blonder B., van Bodegom P.M., Bond-Lamberty B., Campetella G., Cerabolini B.E.L., Chapin F.S., Cornwell W.K., Craine J., Dainese M., de Vries F.T., Díaz S., Enquist B.J., Green W., Milla R., Niinemets Ü., Onoda Y., Ordoñez J.C., Ozinga W.A., Penuelas J., Poorter H., Poschold P., Reich P.B., Sandel B., Schamp B., Sheremetev S., Weiher E. (2018) Plant functional trait change across a warming tundra biome. *Nature*, **562**, 57–62.
- Blondeel H., Perring M.P., Bergès L., Brunet J., Decocq G., Depauw L., Diekmann M., Landuyt D., Liira J., Maes S.L., Vanhellefont M., Wulf M., Verheyen K. (2019) Context-dependency of agricultural legacies in temperate forest soils. *Ecosystems*, **22**, 781–795.
- Bobbink R., Hicks K., Galloway J., Spranger T., Alkemade R., Ashmore M., Bustamante M., Corderby S., Davidson E., Dentener F., Emmett B., Erisman J.W., Fenn M., Gilliam F., Nordin A., Pardo L., De Vries W. (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications*, **20**, 30–59.
- Bobbink R., Tomassen H., Weijters M., van den Berg L., Braun S., Nordin A., Schütz K., Hettelingh J.P. (2015) Chapter 4: effects and empirical critical loads of Nitrogen for Europe. In: de Vries W., Hettelingh J.-P., Posch M. (Eds), *Critical loads and dynamic risk assessments*. Springer, Berlin, Germany, pp 297–326.
- Bolnick D.I., Amarasekare P., Araújo M.S., Bürger R., Levine J.M., Novak M., Rudolf V.H.W., Schreiber S.J., Urban M.C., Vasseur D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.
- Borer E.T., Harpole W.S., Adler P.B., Lind E.M., Orrock J.L., Seabloom E.W., Smith M.D. (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods in Ecology and Evolution*, **5**, 65–73.
- Bossuyt B., Hermy M., Deckers J. (1999) Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. *Journal of Ecology*, **87**, 629–638.
- Bruelheide H., Dengler J., Purschke O., Lenoir J., Jiménez-Alfaro B., Hennekens S.M., Botta-Dukát Z., Chytrý M., Field R., Jansen F., Kattge J., Pillar V.D., Schrod F., Mahecha M.D., Peet R.K., Sandel B., van Bodegom P., Altman J., Alvarez-Dávila E., Arfin Khan M.A.S., Attorre F., Aubin I., Baraloto C., Barroso J.G., Bauters M., Bergmeier E., Biurrun I., Bjorkman A.D., Blonder B., Čarni A., Cayuela L., Černý T., Cornelissen J.H.C., Craven D., Dainese M., Derroire G., De Sanctis M., Díaz S., Doležal J., Farfan-Rios W., Feldpausch T.R., Fenton N.J., Garnier E., Guerin G.R., Gutiérrez A.G., Haider S., Hat-tab T., Henry G., Hérault B., Híguchi P., Hölzel N., Homeier J., Jentsch A., Jürgens N., Kački Z., Karger D.N., Kessler M., Kleyer M., Knollová I., Korolyuk A.Y., Kühn I., Laughlin D.C., Lens F., Loos J., Louault F., Lyubenova M.I., Malhi Y., Marcondé C., Mencuccini M., Müller J.V., Munzinger J., Myers-Smith I.H., Neill D.A., Niinemets Ü., Orwin K.H., Ozinga W.A., Penuelas J., Pérez-Haase A., Petřík P., Phillips O.L., Pärtel M., Reich P.B., Römermann C., Rodrigues A.V., Sabatini F.M., Sardans J., Schmidt M., Seidler G., Silva Espejo J.E., Silveira M., Smyth A., Sporbert M., Svenning J.-C., Tang Z., Thomas R., Tsiripidis I., Vassilev K., Violle C., Vitanen R., Weiher E., Welk E., Wesche K., Winter M., Wirth C., Jandt U. (2018) Global trait–environment relationships of plant communities. *Nature Ecology & Evolution*, **2**, 1906–1907.

- Burton J.I., Perakis S.S., McKenzie S.C., Lawrence C.E., Puettmann K.J. (2017) Intraspecific variability and reaction norms of forest understorey plant species traits. *Functional Ecology*, **31**, 1881–1893.
- Cadotte M.W., Arnillas C.A., Livingstone S.W., Yasui S.-L.E. (2015) Predicting communities from functional traits. *Trends in Ecology & Evolution*, **30**, 510–511.
- Chapin F.S., Shaver G.R. (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology*, **66**, 564–576.
- Craine J.M., Dybzinski R. (2013) Mechanisms of plant competition for nutrients, water and light (D. Robinson, Ed.). *Functional Ecology*, **27**, 833–840.
- De Frenne P., De Schrijver A., Graae B.J., Gruwez R., Tack W., Vandelook F., Hermy M., Verheyen K. (2010) The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. *Ecological Research*, **25**, 163–171.
- De Frenne P., Baeten L., Graae B.J., Brunet J., Wulf M., Orzechowska A., Kolb A., Jansen I., Jamoneau A., Jacquemyn H., Hermy M., Diekmann M., De Schrijver A., De Sanctis M., Decocq G., Cousins S.A.O., Verheyen K. (2011a) Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology*, **99**, 600–609.
- De Frenne P., Graae B.J., Kolb A., Shevtsova A., Baeten L., Brunet J., Chabrierie O., Cousins S.A.O., Decocq G., Dhondt R., Diekmann M., Gruwez R., Heinken T., Hermy M., Öster M., Saguer R., Stanton S., Tack W., Vanhellemont M., Verheyen K. (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., Coomes D.A., De Schrijver A., Staelens J., Alexander J.M., Bernhardt-Römermann M., Brunet J., Chabrierie O., Chiarucci A., den Ouden J., Eckstein R.L., Graae B.J., Gruwez R., Hédl R., Hermy M., Kolb A., Märell A., Mullender S.M., Olsen S.L., Orzechowska A., Peterken G., Petřík P., Plue J., Simonson W.D., Tomescu C.V., Vangansbeke P., Verstraeten G., Vesterdal L., Wulf M., Verheyen K. (2014) Plant movements and climate warming: intraspecific variation in growth responses to nonlocal soils. *New Phytologist*, **202**, 431–441.
- De Frenne P., Rodríguez-Sánchez F., De Schrijver A., Coomes D.A., Hermy M., Vangansbeke P., Verheyen K. (2015) Light accelerates plant responses to warming. *Nature Plants*, **1**, 15110.
- DEIMS-SDR Database (2019) DEIMS-SDR: Dynamic Ecological Information Management System - Site and dataset registry. Available from <https://deims.org/4a469a86-868b-4160-b72e-10a1b4e09356> (accessed 2 July 2019).
- DeMalach N., Zaady E., Weiner J., Kadmon R. (2016) Size asymmetry of resource competition and the structure of plant communities. *Journal of Ecology*, **104**, 899–910.
- Díaz S., Kattge J., Cornelissen J.H.C., Wright I.J., Lavorel S., Dray S., Reu B., Kleyer M., Wirth C., Colin Prentice I., Garnier E., Bönsch G., Westoby M., Poorter H., Reich P.B., Moles A.T., Dickie J., Gillison A.N., Zanne A.E., Chave J., Wright S.J., Sheremet'ev S.N., Jactel H., Baraloto C., Cerabolini B., Pierce S., Shipley B., Kirkup D., Casanoves F., Joswig J.S., Günther A., Falczuk V., Rüger N., Mahecha M.D., Gorné L.D. (2016) The global spectrum of plant form and function. *Nature*, **529**, 167–171.
- Dirnböck T., Foldal C., Djukic I., Kobler J., Haas E., Kiese R., Kitzler B. (2017) Historic nitrogen deposition determines future climate change effects on nitrogen retention in temperate forests. *Climatic Change*, **144**, 221–235.
- Easlon H.M., Bloom A.J. (2014) Easy leaf area: automated digital image analysis for rapid and accurate measurement of leaf area. *Applications in Plant Sciences*, **2**, 1400033.
- Escudero A., Valladares F. (2016) Trait-based plant ecology: moving towards a unifying species coexistence theory. *Oecologia*, **180**, 919–922.
- Evans J.R., Poorter H. (2001) Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell and Environment*, **24**, 755–767.
- Fajardo A., Siefert A. (2018) Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. *Ecology*, **99**, 1024–1030.
- Feng Y., Van Kleunen M. (2014) Responses to shading of naturalized and non-naturalized exotic woody species. *Annals of Botany*, **114**, 981–989.
- Firn J., McGree J.M., Harvey E., Flores-moreno H., Schütz M., Buckley Y.M., Borer E.T., Seabloom E.W., Pierre K.J., La Moudoull A.M., Prober S.M., Stevens C.J., Sullivan L.L., Porter E., Ladouceur E., Allen C., Moromizato K.H., Morgan J.W., Harpole W.S., Hautier Y., Eisenhauer N., Wright J.P., Adler P.B., Brown C.S., Bugalho M.N., Caldeira M.C., Cleland E.E., Ebeling A., Fay P.A., Hagenah N., Klein-hesselink A.R., Mitchell R., Moore J.L., Nogueira C., Peri P.L., Roscher C., Smith M.D., Wragg P.D., Risch A.C. (2019) Leaf nutrients, not specific leaf area, are consistent indicators of elevated nutrient inputs. *Nature Ecology & Evolution*, **4**, 400–406.
- Fraterrigo J.M., Pearson S.M., Turner M.G. (2009) The response of understorey herbaceous plants to nitrogen fertilization in forests of different land-use history. *Forest Ecology and Management*, **257**, 2182–2188.
- Freckleton R.P., Watkinson A.R. (2001) Asymmetric competition between plant species. *Functional Ecology*, **15**, 615–623.
- Funk J.L., Larson J.E., Ames G.M., Butterfield B.J., Cavender-Bares J., Firn J., Laughlin D.C., Sutton-Grier A.E., Williams L., Wright J. (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews*, **92**, 1156–1173.
- Fynn R.W.S., O'Connor T.G. (2005) Determinants of community organization of a South African mesic grassland. *Journal of Vegetation Science*, **16**, 93–102.
- Garnier E., Navas M.L., Grigulis K. (2016) *Plant functional diversity. Organism traits, community structure, and ecosystem properties*. Oxford University Press, Oxford, UK.
- Gilliam F.S. (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience*, **57**, 845–858.
- Gleason H. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7–26.
- Götzenberger L., de Bello F., Bräthen K.A., Davison J., Dubuis A., Guisan A., Lepš J., Lindborg R., Moora M., Pärtel M., Pellissier L., Pottier J., Vittoz P., Zobel K., Zobel M. (2012) Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews*, **87**, 111–127.
- Gross N., Kunstler G., Liancourt P., De Bello F., Suding K.N., Lavorel S. (2009) Linking individual response to biotic interactions with community structure: a trait-based framework. *Functional Ecology*, **23**, 1167–1178.
- Heinken T., Diekmann M., Liira J., Orzechowska A., Brunet J., Chytrý M., Chabrierie O., De Frenne P., Decocq G., Drevojan P., Dzwonko Z., Ewald J., Feilberg J., Graae B.J., Grytnes J.A., Hermy M., Kriebitzsch W.-U., Laivins M., Lindmo S., Marage D., Marozas V., Meirland A., Niemeyer T., Paal J., Prysek P., Roosaluuste E., Sadlo J., Schaminée J.H.J., Schmidt M., Tyler T., Verheyen K., Wulf M. (2019) European forest vascular plant species list. figshare. <https://doi.org/10.6084/m9.figshare.8095217.v1>.
- Hejcman M., Křišťálová V., Červená K., Hrdličková J., Pavlů V. (2012) Effect of nitrogen, phosphorus and potassium availability on mother plant size, seed production and germination ability of *Rumex crispus*. *Weed Research*, **52**, 260–268.
- Helsen K., Acharya K.P., Brunet J., Cousins S.A.O., Decocq G., Hermy M., Kolb A., Lemke I.H., Lenoir J., Plue J., Verheyen K., De Frenne P., Graae B.J. (2017) Biotic and abiotic drivers of intraspecific trait variation within plant populations of three herbaceous plant species along a latitudinal gradient. *BMC Ecology*, **17**, 1–12.
- Henn J.J., Buzzard V., Enquist B.J., Halbritter A.H., Klanderud K., Maitner B.S., Michalet S.T., Pötsch C., Seltzer L., Telford R.J., Yang Y., Zhang L., Vandvik V. (2018) Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, **9**, 1548.
- Henneron L., Chauvat M., Archaux F., Akpa-Vinceslas M., Bureau F., Dumas Y., Mignot L., Ningre F., Perret S., Richter C., Balandier P., Aubert M. (2017) Plant interactions as biotic drivers of plasticity in leaf litter traits and decomposability of *Quercus petraea*. *Ecological Monographs*, **87**, 321–340.
- Hoepfner S.S., Dukes J.S. (2012) Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology*, **18**, 1754–1768.
- Hollister R.D., Webber P.J., Bay C. (2005) Plant response to temperature in Northern Alaska: Implications for predicting vegetation change. *Ecology*, **86**, 1562–1570.
- Jagodziński A.M., Dyderski M.K., Rawlik K., Katna B. (2016) Seasonal variability of biomass, total leaf area and specific leaf area of forest understorey herbs reflects their life strategies. *Forest Ecology and Management*, **374**, 71–81.
- Jung V., Violle C., Mondy C., Hoffmann L., Muller S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**, 1134–1140.
- Kahl S.M., Lenhard M., Joshi J. (2019) Compensatory mechanisms to climate change in the widely distributed species *Silene vulgaris*. *Journal of Ecology*, **107**, 1918–1930.
- Klímešová J., Tackenberg O., Herben T. (2016) Herbs are different: clonal and bud bank traits can matter more than leaf–height–seed traits. *New Phytologist*, **210**, 13–17.
- Kollmann J., Bañuelos M.J. (2004) Latitudinal trends in growth and phenology of the invasive alien plant *Impatiens glandulifera* (Balsaminaceae). *Diversity and Distributions*, **10**, 377–385.
- Lajoie G., Vellend M. (2015) Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching. *Ecology*, **96**, 2912–2922.

- Lajoie G., Vellend M. (2018) Characterizing the contribution of plasticity and genetic differentiation to community-level trait responses to environmental change. *Ecology and Evolution*, **8**, 3895–3907.
- Landuyt D., Perring M.P., Seidl R., Taubert F., Verbeeck H., Verheyen K. (2018) Modelling understorey dynamics in temperate forests under global change – challenges and perspectives. *Perspectives in Plant Ecology, Evolution and Systematics*, **31**, 44–54.
- Laughlin D.C., Leppert J.J., Moore M.M., Sieg C.H. (2010) A multi-trait test of the leaf–height–seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, **24**, 493–501.
- Laughlin D.C., Joshi C., van Bodegom P.M., Bastow Z.A., Fulé P.Z. (2012) A predictive model of community assembly that incorporates intraspecific trait variation (T. Fukami, Ed.). *Ecology Letters*, **15**, 1291–1299.
- Le Bagousse-Pinguet Y., Börger L., Quero J.-L., García-Gómez M., Soriano S., Maestre F.T., Gross N. (2015) Traits of neighbouring plants and space limitation determine intraspecific trait variability in semi-arid shrublands. *Journal of Ecology*, **103**, 1647–1657.
- Lemke I.H., Kolb A., Graae B.J., De Frenne P., Acharya K.P., Blandino C., Brunet J., Chaberrie O., Cousins S.A.O., Decocq G., Heinken T., Hermy M., Liira J., Schmucki R., Shevtsova A., Verheyen K., Diekmann M. (2015) Patterns of phenotypic trait variation in two temperate forest herbs along a broad climatic gradient. *Plant Ecology*, **216**, 1523–1536.
- Lipowsky A., Roscher C., Schumacher J., Michalski S.G., Gubsch M., Buchmann N., Schulze E.D., Schmid B. (2015) Plasticity of functional traits of forb species in response to biodiversity. *Perspectives in Plant Ecology, Evolution and Systematics*, **17**, 66–77.
- Liu Y., Dawson W., Prati D., Haeuser E., Feng Y., van Kleunen M. (2016) Does greater specific leaf area plasticity help plants to maintain a high performance when shaded? *Annals of Botany*, **118**, 1329–1336.
- Luo Y., Melillo J., Niu S., Beier C., Clark J.S., Classen A.T., Davidson E., Dukes J.S., Evans R.D., Field C.B., Czimczik C.I., Keller M., Kimball B.A., Kueppers L.M., Norby R.J., Pelini S.L., Pendall E., Rastetter E., Six J., Smith M., Tjoelker M.G., Torn M.S. (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology*, **17**, 843–854.
- Mabry C.M., Gerken M.E., Thompson J.R. (2008) Seasonal storage of nutrients by perennial herbaceous species in undisturbed and disturbed deciduous hardwood forests. *Applied Vegetation Science*, **11**, 37–44.
- Mao W., Felton A.J., Zhang T. (2017) Linking changes to intraspecific trait diversity to community functional diversity and biomass in response to snow and nitrogen addition within an inner Mongolian grassland. *Frontiers in Plant Science*, **8**, 1–10.
- Midolo G., De Frenne P., Hölzel N., Wellstein C. (2019) Global patterns of intraspecific leaf trait response to elevation. *Global Change Biology*, **25**, 2485–2498.
- Milla R., Reich P.B. (2007) The scaling of leaf area and mass: The cost of light interception increases with leaf size. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **274**, 2109–2114.
- Moles A.T., Warton D.I., Warman L., Swenson N.G., Laffan S.W., Zanne A.E., Pitman A., Hemmings F.A., Leishman M.R. (2009) Global patterns in plant height. *Journal of Ecology*, **97**, 923–932.
- Moran E.V., Hartig F., Bell D.M. (2016) Intraspecific trait variation across scales: Implications for understanding global change responses. *Global Change Biology*, **22**, 137–150.
- Muukkonen P., Mäkipää R., Laiho R., Minkinen K., Vasander H., Finér L. (2006) Relationship between biomass and percentage cover in understorey vegetation of boreal coniferous forests. *Silva Fennica*, **40**, 231–245.
- Nagashima H., Hikosaka K. (2011) Plants in a crowded stand regulate their height growth so as to maintain similar heights to neighbours even when they have potential advantages in height growth. *Annals of Botany*, **108**, 207–214.
- Navas M.L., Garnier E. (2002) Plasticity of whole plant and leaf traits in *Rubia peregrina* in response to light, nutrient and water availability. *Acta Oecologica*, **23**, 375–383.
- Nicolson M., McIntosh R.P. (2002) H. A. Gleason and the individualistic hypothesis revisited summary. *Bulletin of the Ecological Society of America*, **83**, 133–142.
- Oldfather M.F. (2019) Ecoregion shapes the range response. *Nature Climate Change*, **9**, 730–731.
- Oliver T.H., Morecroft M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, **5**, 317–335.
- Ott J.P., Klimešová J., Hartnett D.C. (2019) The ecology and significance of below-ground bud banks in plants. *Annals of Botany*, **123**, 1099–1118.
- Paul-Limoges E., Wolf S., Eugster W., Hörtnagl L., Buchmann N. (2017) Below-canopy contributions to ecosystem CO₂ fluxes in a temperate mixed forest in Switzerland. *Agricultural and Forest Meteorology*, **247**, 582–596.
- Pérez-Harguindeguy N., Díaz S., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M.S., Cornwell W.K., Craine J.M., Gurvich D.E., Urcelay C., Veneklaas E.J., Reich P.B., Poorter L., Wright I.J., Ray P., Enrico L., Pausas J.G., de Vos A.C., Buchmann N., Funes G., Quétier F., Hodgson J.G., Thompson K., Morgan H.D., ter Steege H., Van Der Heijden M.G.A., Sack L., Blonder B., Poschlod P., Vaieretti M.V., Conti G., Staver A.C., Aquino S., Cornelissen J.H.C. (2013) New handbook for standardized measurement of plant functional traits worldwide. *Australian Journal of Botany*, **23**, 167–234.
- Perring M.P., De Frenne P., Baeten L., Maes S.L., Depauw L., Blondeel H., Carón M.M., Verheyen K. (2016) Global environmental change effects on ecosystems: the importance of land-use legacies. *Global Change Biology*, **22**, 1361–1371.
- Perring M.P., Bernhardt-Römermann M., Baeten L., Midolo G., Blondeel H., Depauw L., Landuyt D., Maes S.L., De Lombaerde E., Carón M.M., Vellend M., Brunet J., Chudomelová M., Decocq G., Diekmann M., Dirnböck T., Dörfler I., Durak T., De Frenne P., Gilliam F.S., Hédli R., Heinken T., Hommel P., Jaroszewicz B., Kirby K.J., Kopecký M., Lenoir J., Li D., Málíš F., Mitchell F.J.G., Naaf T., Newman M., Petřík P., Reczyńska K., Schmidt W., Standovář T., Świerkosz K., Van Calster H., Vild O., Wagner E.R., Wulf M., Verheyen K. (2018a) Global environmental change effects on plant community composition trajectories depend upon management legacies. *Global Change Biology*, **24**, 1722–1740.
- Perring M.P., Diekmann M., Midolo G., Schellenberger Costa D., Bernhardt-Römermann M., Otto J.C.J., Gilliam F.S., Hedwall P.O., Nordin A., Dirnböck T., Simkin S.M., Málíš F., Blondeel H., Brunet J., Chudomelová M., Durak T., De Frenne P., Hédli R., Kopecký M., Landuyt D., Li D., Manning P., Petřík P., Reczyńska K., Schmidt W., Standovář T., Świerkosz K., Vild O., Waller D.M., Verheyen K. (2018b) Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. *Environmental Pollution*, **242**, 1787–1799.
- Pinheiro J., Bates D., DebRoy S., Sarkar D., R Core Team (2019) *nlme: linear and nonlinear mixed effects models. R package version 3.1–143*. R Foundation for Statistical Computing, Vienna, Austria.
- Poorter H., Niinemets Ü., Poorter L., Wright I.J., Villar R., Niinemets U., Poorter L., Wright I.J., Villar R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.
- R Core Team (2019) R: A language and environment for statistical computing. Available from <https://www.r-project.org/> (accessed 5 October 2019).
- Reich P.B. (2014) The world-wide ‘fast-slow’ plant economic spectrum: a traits manifesto (H. Cornelissen, Ed.). *Journal of Ecology*, **102**, 275–301.
- Reich P.B., Wright I.J., Craine J.M., Oleksyn J., Westoby M., Walters M.B. (2003) The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences*, **164**, S143–S164.
- Rothstein D.E. (2000) Spring ephemeral herbs and nitrogen cycling in a northern hardwood forest: an experimental test of the vernal dam hypothesis. *Oecologia*, **124**, 446–453.
- Rothstein D.E., Zak D.R. (2001) Photosynthetic adaptation and acclimation to exploit seasonal periods of direct irradiance in three temperate, deciduous-forest herbs. *Functional Ecology*, **15**, 722–731.
- Rozendaal D.M.A., Hurtado V.H., Poorter L. (2006) Plasticity in leaf traits of 38 tropical tree species in response to light: relationships with light demand and adult stature. *Functional Ecology*, **20**, 207–216.
- Siefert A. (2012) Spatial patterns of functional divergence in old-field plant communities. *Oikos*, **121**, 907–914.
- Siefert A., Ritchie M.E. (2016) Intraspecific trait variation drives functional responses of old-field plant communities to nutrient enrichment. *Oecologia*, **181**, 245–255.
- Siefert A., Violle C., Chalmandrier L., Albert C.H., Taudiere A., Fajardo A., Aarssen L.W., Baraloto C., Carlucci M.B., Cianciaruso M.V., de L Dantas V., de Bello F., Duarte L.D.S., Fonseca C.R., Freschet G.T., Gaucherand S., Gross N., Hikosaka K., Jackson B., Jung V., Kamiyama C., Katabuchi M., Kembel S.W., Kichenin E., Kraft N.J.B., Lagerström A., Bagousse-Pinguet Y.L., Li Y., Mason N., Messier J., Nakashizuka T., Overton J.M., Peltzer D.A., Pérez-Ramos I.M., Pillar V.D., Prentice H.C., Richardson S., Sasaki T., Schamp B.S., Schöb C., Shipley B., Sundqvist M., Sykes M.T., Vandewalle M., Wardle D.A. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, **18**, 1406–1419.
- Smart S.M., Gланville H.C., Blanes M. del C., Mercado L.M., Emmett B.A., Jones D.L., Cosby B.J., Marrs R.H., Butler A., Marshall M.R., Reinsch S., Herrero-Jáuregui C., Hodgson J.G. (2017) Leaf dry matter content is better at predicting above-ground net

- primary production than specific leaf area. *Functional Ecology*, **31**, 1336–1344.
- Tatarko A.R., Knops J.M.H. (2018) Nitrogen addition and ecosystem functioning: Both species abundances and traits alter community structure and function. *Ecosphere*, **9**, e02087.
- Tessier J.T., Raynal D.J. (2003) Vernal nitrogen and phosphorus retention by forest understory vegetation and soil microbes. *Plant and Soil*, **256**, 443–453.
- Thomson F.J., Moles A.T., Auld T.D., Kingsford R.T. (2011) Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, **99**, 1299–1307.
- Turcotte M.M., Levine J.M. (2016) Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*, **31**, 803–813.
- Valladares F., Niinemets Ü. (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 237–257.
- Valladares F., Balaguer L., Martinez-Ferri E., Perez-Corona E., Manrique E. (2002) Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? *New Phytologist*, **156**, 457–467.
- Valladares F., Sanzceg-Gomez D., Zavala M.A. (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology*, **94**, 1103–1116.
- Valladares F., Laanisto L., Niinemets Ü., Zavala M.A. (2016) Shedding light on shade: ecological perspectives of understory plant life. *Plant Ecology & Diversity*, **9**, 237–251.
- Veresoglou S.D., Penuelas J. (2019) Variance in biomass-allocation fractions is explained by distribution in European trees. *New Phytologist*, **222**, 1352–1363.
- Verheyen K., Honnay O., Motzkin G., Hermy M., Foster D.R. (2003) Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology*, **91**, 563–577.
- Verheyen K., De Frenne P., Baeten L., Waller D.M., Hédli R., Perring M.P., Blondeel H., Brunet J., Chudomelová M., Decocq G., De Lombaerde E., Depauw L., Dirnböck T., Durak T., Eriksson O., Gilliam F.S., Heinken T., Heinrichs S., Hermy M., Jaroszewicz B., Jenkins M.A., Johnson S.E., Kirby K.J., Kopecký M., Landuyt D., Lenoir J., Li D., Macek M., Maes S.L., Máliš F., Mitchell F.J.G., Naaf T., Peterken G., Petřík P., Reczyńska K., Rogers D.A., Schei F.H., Schmidt W., Standovář T., Świerkosz K., Ujházy K., Van Calster H., Vellend M., Vild O., Woods K., Wulf M., Bernhardt-Römermann M. (2017) Combining biodiversity resurveys across regions to advance global change research. *BioScience*, **67**, 73–83.
- Verstraeten G., Baeten L., Van den Broeck T., De Frenne P., Demey A., Tack W., Muys B., Verheyen K. (2013) Temporal changes in forest plant communities at different site types. *Applied Vegetation Science*, **16**, 237–247.
- Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I., Garnier E. (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.
- Watkinson A.R. (1983) Yield–density relationships: The influence of resource availability on growth and self-thinning in populations of *Vulpia fasciculata*. *Annals of Botany*, **53**, 469–482.
- Westneat D.F., Potts L.J., Sasser K.L., Shaffer J.D. (2019) Causes and consequences of phenotypic plasticity in complex environments. *Trends in Ecology & Evolution*, **34**, 555–568.
- Westoby M. (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Wright I.J., Westoby M., Reich P.B., Oleksyn J., Ackery D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Gulias J., Garnier E., Navas M.L., Roumet C., Groom P.K., Lamont B.B., Hikosaka K., Lee T., Lee W., Lusk C., Midgley J.J., Niinemets Ü., Osada H., Poorter H., Pool P., Veneklaas E.J., Prior L., Pyankov V.I., Thomas S.C., Tjoelker M.G., Villar R. (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.
- Wright I.J., Dong N., Maire V., Prentice I.C., Westoby M., Díaz S., Gallagher R.V., Jacobs B.F., Kooyman R., Law E.A., Leishman M.R., Niinemets Ü., Reich P.B., Sack L., Villar R., Wang H., Wilf P. (2017) Global climatic drivers of leaf size. *Science*, **357**, 917–921.
- Wulf M. (1997) Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science*, **8**, 635–642.
- Zhou X., Guo Z., Zhang P., Du G. (2018) Shift in community functional composition following nitrogen fertilization in an alpine meadow through intraspecific trait variation and community composition change. *Plant and Soil*, **431**, 289–302.