RESEARCH ARTICLE

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Trait variation in juvenile plants from the soil seed bank of temperate forests in relation to macro- and microclimate

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Abstract

Aim: The soil seed bank is a key component of the biodiversity of plant communities, but various aspects of its functioning in temperate forest ecosystems are still unknown. We here adopted a trait-based approach to investigate the effects of macro- and microclimatic gradients on the juvenile plant communities from the realized seed bank of two types of European temperate forest.

Location: Oak-dominated forests in Italy and Belgium.

Methods: We analysed the variation of key functional traits (plant height, leaf area, leaf dry weight, specific leaf area and leaf number) of juvenile plants from the realised soil seed bank in relation to elevation (from 0 to 800 m a.s.l.), forest type (thinned and unthinned forest) and distance to the forest edge. We translocated soil samples from the forest core to the edge (and vice versa) and from high- to low-elevation forests to test the effects of edge and warming respectively.

Results: Taller communities developed at the forest edge due to higher light availability and warmer temperatures. The translocation from the core to the edge did not significantly modify mean trait values. Instead, the shadier and cooler microclimate of the forest core reduced the mean leaf area, mean dry weight, height and leaf number in the communities realised from the edge soil. The translocation from high- to lowland forests led to increased values for all traits (except specific leaf area). Edge vs core trait variation was more driven by intraspecific variability, whereas the translocation from high- to low-elevation forests caused trait changes mostly due to species turnover.

Conclusions: Global warming might result in a functional shift of the understorey due to both an early filtering effect on the seedlings from soil seed banks and their adaptive trait adjustments to temperature increase. Furthermore, our study underpins the importance of edge vs core microclimate in driving the functional composition of the realised soil seed bank.

Applied Vegetation Science

1 | INTRODUCTION

Organisms living below or within tree canopies experience climatic conditions that are different from those outside forests. In forests, temperature extremes are buffered, and direct sunlight and wind speed are strongly reduced compared to open habitats (Von Arx et al., 2013; De Frenne et al., 2019). Thanks to the microclimatic effects that they bring about, forest canopies may offer refugia to many understorey species under climate-warming scenarios (Hylander et al., 2015). The buffering capacity of a forest varies greatly depending on forest structure or macroclimate (e.g. it is stronger in warmer climates) and is reduced at the particular microclimatic conditions of the forest edge (McLaughlin et al., 2017; De Frenne et al., 2019; Meeussen et al., 2021).

European forests are strongly fragmented, which implies the existence of a very large proportion of forest edge habitat (40% of Europe's forest habitat is less than 100 m from an edge; Estreguil et al., 2013). Local differences in microclimatic conditions are especially pronounced near forest edges, with higher light availability and wind speeds that make them more susceptible to temperature variability, temperature extremes and drought stress compared to interiors (Davies-Colley et al., 2000; Smith et al., 2019; Meeussen et al., 2021). Altered microclimatic conditions in forest edges create gradients in understorey biodiversity towards the forest core and induce the establishment of communities with a high proportion of generalist species (Ries & Sisk, 2004; De Smedt et al., 2019; Govaert et al., 2020). Forest fragmentation and the following increasing proportion of forest edges could also change ecosystem functioning and accelerate the current homogenisation of understorey plant communities (Staude et al., 2020), likely amplifying the negative consequences of climate change on forest ecosystems (Hofmeister et al., 2019).

So far, the effects of microclimate have been studied on the above-ground vegetation (Pellissier et al., 2013; Zellweger et al., 2020; De Pauw et al., 2021). On the contrary, little is still known about the responses of the soil seed bank to climate change and habitat fragmentation. This is a serious gap since soil seed banks are potential 'biodiversity reservoirs' to maintain and re-establish populations under favourable conditions (Parker & Kelly, 1989). Soil seed banks can contribute to local population persistence and biodiversity maintenance through temporal storage effects (Faist et al., 2013; Plue, De Frenne, et al., 2017), remnant populations (Eriksson, 1996; Plue et al., 2008) and the maintenance of a functional diverse below-ground species pool available for germination in response to environmental variability or change (Del Cacho & Lloret, 2012; Vandvik et al., 2016). The study of the realised soil seed bank (i.e., the seedlings assemblage emerging under field conditions) is especially important as it can provide very different results from greenhouse experiments (i.e., potential soil seed bank), which often favour light-demanding species (Panufnik-Mędrzycka & Kwiatkowska-Falińska, 2014).

To our knowledge, the functional traits of juvenile plants and seedlings emerged from the forest soil seed bank were never investigated before, and no studies assessed whether changes in these traits can occur at the initial recruitment stage in seedlings from the soil seed bank in response to microclimatic variations. Functional-trait approaches can help to understand the processes underlying variation in the realised seed bank, and its potential contribution to community dynamics and adaptive capacity (Larson & Suding, 2022). Indeed, if seed banks store traits that are more advantageous or vulnerable under future conditions, they could impact community composition and adaptability to change and disturbance (Larson & Suding, 2022). For instance, understanding changes in key traits related to resource acquisition, such as plant height and specific leaf area (SLA) can add important information and help to address how the soil seed bank community responds to environmental variations. Previous research demonstrated that temperature increase favours taller plants in the understorey (De Frenne, 2015; Blondeel et al., 2020). Inconsistent responses were instead found for community mean SLA (Dubuis et al., 2013; Depauw et al., 2020; Maes et al., 2020), despite a general decrease under intensified dry conditions (Poorter et al., 2009; Wellstein et al., 2017). Also, the higher light availability at the edge of temperate forests was found to influence the functional responses of the herb communities, with a positive effect on plant height and contrasting effect on SLA, depending on the macroclimatic region (Poorter et al., 2009; De Pauw et al., 2022). The study of intraspecific trait variation (ITV) is relevant to better understand whether and how individual plants can adapt to environmental variation in the short and long term (Siefert et al., 2015; Des Roches et al., 2018), a crucial aspect in this time of global change affecting forests. Seedlings and juvenile plants are more vulnerable to global changes than adult plants (Lloret et al., 2004; Dalgleish et al., 2010), and their survival and development largely depend on the trait responses to external conditions during the delicate early stages of their life.

Here, we explored how the functional composition of realised soil seed banks varies with macro- and microclimate associated with elevation, forest structure and distance to the forest edge, which are considered as factors of seed bank shifts (Luo et al., 2017; Zou et al., 2021). Moreover, we included two European climatic regions, Italy and Belgium. Using a translocation experiment from high- to low-elevation sites, we also exposed the forest seed banks to a temperature increase in the range predicted by the current projections for the next decades. We focused on plant height and SLA since these functional traits reflect relevant aspects of plant growth, performance and function (Westoby, 1998; Díaz et al., 2016).

Additionally, leaf area and leaf dry weight were investigated to unravel their contribution to the variation (or not) in SLA. Finally, leaf number was also considered because of the relationship between this trait and plant survival (Berg & Redbo-torstensson, 1998). We hypothesized that:

> **H1.** The functional composition of the realised soil seed bank varies along macro- and microclimatic gradients with a different contribution of inter- and intraspecific variability. Specifically, edge microclimate enhances the establishment of taller seedling communities with lower SLA;

> **H2.** Experimental warming (via translocation from high to low elevation) favours the development from the soil seed bank of taller plants with more leaves, but with a lower SLA;

> **H3.** Responses differ between species and depend on the ecological group these species belong to, that is forest specialists versus generalists.

2 | MATERIALS AND METHODS

2.1 | Study area

The experiment was set up in two European regions: Italy (42°N, 11°E) and Belgium (50°N, 5°E) (Appendix A1 in the Supporting Information), covering the submediterranean and temperate forest biomes respectively. The study design was replicated along an elevational gradient represented by lowland (21–140 m) and highland (312–798 m) sites. At each site (Figure 1), a thinned and an unthinned forest stand were selected. Unthinned forests are dense stands, with uneven-aged trees and shrubs, high canopy cover (trees + shrubs > 120%), high basal area (between 19 and 52 m^2 ha^{-1}) and a well-developed shrub layer. Unthinned forests were not thinned for at least 30 years. Thinned forests were typically open, even-aged stands, with a lower basal area (8–24 m^2/ha^{-1}), lower canopy cover (trees + shrubs < 100%) and a sparse or absent shrub layer. Thinning (i.e., low thinning: to convert old coppices-with-standard to high forest through the selection of one stem per stump) was done recently (within six years from sampling). In each stand, two plots were selected, one at the forest edge and another one at the forest core (100 m from the edge). We thus established 16 experimental plots in total, in two regions (Italy and Belgium), at two elevations (high and low elevation), in two forest types (thinned and unthinned) and in two positions (edge vs core) (Figure 1). The selected stands belong to mesic (Belgium) and thermophilous (Italy) deciduous forests dominated by oak species. In Italy, dominant tree species were *Quercus cerris* L. with presence of *Fraxinus ornus* L, *Ostrya carpinifolia* Scop. and *Prunus avium* (L.) L. In Belgium dominant trees were *Quercus robur* L., *Quercus petraea* (Matt.) Liebl., *Quercus rubra* L., *Fagus sylvatica* L., *Acer pseudoplatanus* L. and *Carpinus betulus*. All the edges were south-facing, bordered by grassland or arable land and were mostly maintained as cantilevered edges (edge maintained at the first line of tree trunks). For site descriptions see Appendix A2 in the Supporting Information.

2.2 | Experimental setup

Between January and February 2020, we collected soil samples in two quadrats (2 m × 2 m) at the forest edge (0.5 m from the forest
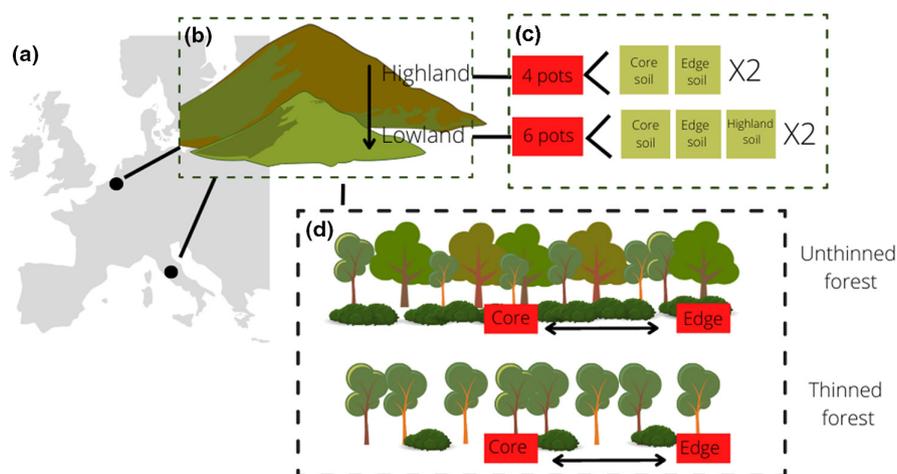

FIGURE 1 Experimental design: (a) location of the experimental regions (black circles) in Italy and Belgium; (b) highland and lowland sites; (c) each experimental plot contains four or six pots depending on highland or lowland position respectively: edge soil is soil collected in the forest edge, core soil is soil collected in the forest core, highland soil is soil collected in highland forests (respectively at the edge or at the core). Arrows show the translocation of soil to the forest edge and core and from high- to low-elevation forests; (d) arrangement of the plots at the forest edge and at the forest core of thinned and unthinned stands. This design resulted in eight edge-to-core sites (16 experimental plots): [8 highland plots × 4 pots] + [8 lowland plots × 6 pots].

edge) and in two quadrats at the forest core in all eight sites (16 experimental plots in total, Figure 1). Within each quadrat, we randomly collected 60 and 45 soil samples (5 cm × 4 cm, litter removed), resulting in a soil volume of ca. 4.7 and 3.7 L for the high- and the low-elevation forest respectively. Soil samples collected within each quadrat were mixed and divided into three portions in the low-elevation sites and four portions in the high-elevation sites. Each portion of soil equally consisted of ca. 0.9 L and, after sieving with a 4-mm sieve, was laid on the top of a 15 cm deep layer of sterilised potting soil in pots (30 cm × 20 cm) such that the forest soil layer was ca. 1 cm thick. At each position (edge and core), one experimental plot was installed between the two quadrats. There, the pots with the sieved forest soil samples were placed at the edge and forest core in the original and exchanged positions (Figure 1), for a total of 80 pots (40 treatments, with two replicates for each treatment). Specifically, two pots (as two replicates) always remained in place and two were moved from the forest edge to the forest core, and vice versa. For the high-elevation forest, two more pots for each position (edge and core) and for each forest type were brought to the low-elevation forest and placed in the corresponding forest type and in the corresponding edge or core position. Finally, one portion of soil was brought to a greenhouse and kept in ambient conditions to check and facilitate plant identification in the field. For more detailed information on soil sample collection see also Gasperini et al. (2021).

2.3 | Translocation from high- to low-elevation forest

Through the translocation of the soil samples from high- to low-elevation forests, we simulated an increase in soil and air temperature of approximately 2–3°C for Italy and 1–2°C for Belgium. These values correspond to the predicted land temperature increase under different climate change scenarios for Europe by the end of 2100 (1.5°C, 2.4°C and 4.1°C under the RCP2.6, RCP4.5 and RCP8.5 scenarios respectively) (Gutiérrez et al., 2021). Air and soil temperatures were recorded at each experimental plot at hourly intervals (2018–2020) using a Lascar temperature logger (EasyLog EL-USB-1, accuracy at −35 to +80°C: ±0.5°C). Air loggers were placed at 1 m height in a white plastic radiation shield (see also Meeussen et al. (2021)). Soil loggers were buried in the ground in a plastic tube at 5 cm depth. The mean soil and air temperature increase was calculated as the difference between mean soil and air temperature in high- and low-elevation forests, separately for thinned and unthinned forests (for details see Appendix A3 in the Supporting Information).

2.4 | Field surveys

Measurements in the experimental plots were done in April 2020 (to account for species emerging in early spring) and repeated in July 2020. Each seedling was identified (species nomenclature follows Euro+Med, 2006) and mapped on a 5 cm × 5 cm grid laid down on the box soil surface. This allowed to measure the same individuals of each species in the first and second surveys and to check whether the individual was already present in April or emerged later. The total height, without stretching, and the total number of leaves were measured for each individual. In July, one large and healthy leaf was collected for each individual and oven-dried at 40°C for 48 h. Leaves were scanned to measure their area with an LI-3100C Area Meter (Li-Cor Environmental, Lincoln, NE, USA) and weighed (to 0.1 mg). SLA was calculated by dividing the leaf area (LA) by the oven-dried leaf mass (mm^2/mg^{-1}).

2.5 | Data analyses

All analyses were performed in the R environment (R Core Team, 2022). Direct measurements on all seedlings emerging from the seed bank (for the spring and summer surveys, April and July respectively) were used in the models (ca. 1550 observations) and analysed with generalized linear mixed-effect models using template model builder and linear mixed-effects models (glmmTMB and LMMs). Response variables are thus mean values of species trait (without species cover). The models were fitted using the packages *lme4* (Bates et al., 2015), *MuMIn* (Bartoń, 2019), *glmmTMB* (Brooks et al., 2017) and *bbmle* (Bolker and R Core Team, 2021). Mean and standard deviations of plant height, leaf dry weight, leaf area, SLA and number of leaves per treatment are given in Appendix A4 in the Supporting Information. The responses of plant height, leaf dry weight, leaf area, SLA and leaf number were analysed in relation to the following explanatory variables: edge vs core vs translocated soil (edge soil in the edge position vs edge soil in the core position vs core soil in core position vs core soil in edge position); region (Belgium vs Italy); forest type (thinned vs unthinned) and elevation (high elevation vs high to low elevation vs low elevation).

Given the frequent zero-valued observations and overdispersion, a zero inflated model with a negative binomial distribution (*glmmTMB*) was used for the number of leaves (count data). The best fitting distribution was tested with the AICtab of package *bbmle* (Bolker, 2021). For the other response variables, a Gaussian distribution was applied, resulting in linear mixed-effect models (LMMs). The leaf area, leaf dry weight and SLA were left-skewed and thus were log-transformed before modelling to increase normality. All fixed effects were categorical variables. For the sake of simplicity, only interactions between edge vs core and region were considered. In all models, 'site' (see Figure 1) was added as a random effect term to account for spatial autocorrelation due to the hierarchical structure of the data. Also 'species' was added as a random effect to account for interspecific variation. The following equation represents the starting model:

$$\text{Variable} \sim \text{edge vs core vs translocated soil} + \text{region} + \text{elevation} + \text{forest type} + \text{region: edge vs core vs translocated soil} + (1|\text{site/species}).$$

The single best model was selected based on lower Akaike information criterion (AIC) and Bayesian information criterion (BIC)

FIGURE 2 Violin plots showing variation in mean values of species trait (without species cover) from the realised soil seed bank between regions (a–e), highland vs lowland (f–l) and thinned and unthinned forests (m–q) for plant height, leaf area, leaf dry weight, SLA and leaf number. The mean of leaf area, leaf dry weight and specific leaf area (SLA) were log-transformed for the analysis and back-transformed into the original scale for data visualisation. The significance of *p-values* is given as ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; and refers to the models' results (Table 1).
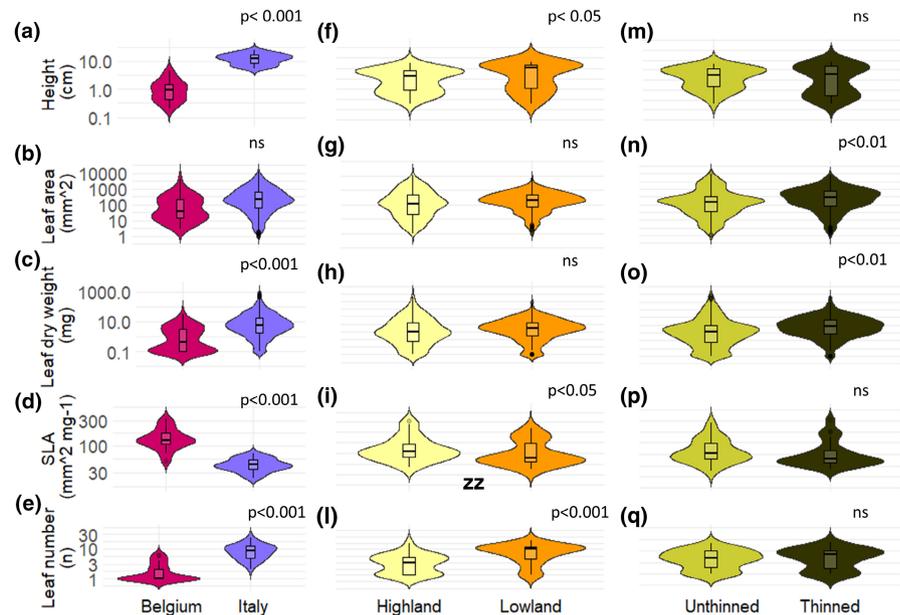
displaying a selection of models with delta AIC < 2 with the 'dredge' function of package *MuMIn* (Bartoń, 2019). In all models, residuals were evaluated for normality and homogeneity by a visual check of the model assumptions (normality of residuals, normality of random effects, homogeneity of variance). For all models, we computed the proportion of variance explained by the fixed effects of the model (marginal R^2) and by both random and fixed effects (conditional R^2) (Nakagawa & Schielzeth, 2013). The comparison between core soil in core position vs core soil in edge position was done running the same set of models but changing the reference category, that is, changing the category of comparison used in the model (Appendix A5 in the Supporting Information).

To understand how the observed variation was related to intra- or interspecific trait variation, we assessed the amount of trait variation explained by species turnover, ITV or covariation based on the sum of squares of the linear mixed-effect models following the method of Lepš et al. (2011). To exclude ITV a community-weighted mean was calculated based on the mean trait value per species across all boxes (CWMfixed). Then, a community-weighted mean that accounted for intraspecific variability (CWMspecific) was calculated by weighting each plant trait per box (averaged across all individuals in a box) with the mean percentage ground cover of the species per box. Finally, the CWMitv was derived as CWMspecific − CWMfixed. The covariation was calculated as Total variation (CWMspecific) − species turnover (CWMfixed) − ITV (CWMitv). When the covariation is close to zero, turnover and ITV act on the trait CWM independently. When the covariation is positive, turnover and ITV are positively correlated (i.e., when high fixed average values are accompanied by positive intraspecific variability effect, and vice vera (Lepš et al., 2011)). When the covariation is negative, turnover and ITV are negatively correlated.

Then, to assess the influence of our predictors on the different sources of community variation. we tested the CWMfixed, CWMitv and CWMspecific for plant height, leaf number and SLA in the subsequent model:

Variable ~ edge vs core vs translocated soil + region + elevation + forest type + region: edge vs core vs translocated soil + (1|site).

The same analysis and procedure for model selection as above were repeated.

Additionally, to assess the ITV in relation to treatments (focussing on translocation of soil from highland to lowland and from the edge to the core and vice versa), a total of 24 species (eight forest herbs and 16 habitat generalists) were analysed with an ANOVA or Kruskal–Wallis test, depending on data normality (Table 2). The recorded species were assigned to four forest guilds following the classification proposed by Heinken et al. (2022) (see Appendix A6 in the Supporting Information). The proportion of missing values across all species and traits was 1.4%. The hypothesis of normality of distribution was tested with the Lilliefors (Kolmogorov–Smirnov) test with the function 'lillie.test' in the package *nortest*. Homogeneity of variances was tested with Bartlett's test with the function *bartlett. test*. One-way ANOVA was performed with the 'aov' function followed by a post-hoc Tukey's honestly significant difference (HSD) test with the *TukeyHSD* function. A Kruskal–Wallis test was performed with the 'kruskal.test' function followed by a Dunn's post-hoc test, made with the 'dunn.test' function in the *dunn.test* package.

3 | RESULTS

3.1 | Trait responses in seedling communities from the seed bank

We found significant differences in the responses of the seedling assemblages that emerged from the soil placed in the original position along the considered gradients. Mean plant height, leaf number and leaf dry weight were higher in Italy (Figure 2a,c,e), whereas mean SLA

was higher in Belgium (Figure 2d). Additionally, lowland forests had lower mean SLA but a higher plant height and leaf number compared to high-elevation forests (Figure 2f,i,l). Forest structure affected leaf area and leaf dry weight, as both showed higher mean values in thinned forests (Figure 2n,o). Finally, the only strong response that we observed between edge vs core communities (Figure 3) was a lower mean plant height at the forest core.

3.2 | Effects of edge vs core microclimate and highland vs lowland translocation on seedling communities

All traits, except SLA, decreased in soil translocated from the forest edge to the core (Figure 3). On the contrary, with the translocation from the forest core to the edge we generally observed no variation in mean trait values, with the exception of leaf dry weight, which slightly increased (Figure 3b). The negative interaction between Italy and the core to edge translocation indicates that in this region, the mean number of leaves was lower in the core soil translocated to the edge (compared to the edge soil placed in edge, Table 1), whereas this was not the case in Belgium. Finally, all traits except SLA responded to the translocation of soil from high- to low-elevation forests with increasing values (Figure 4).
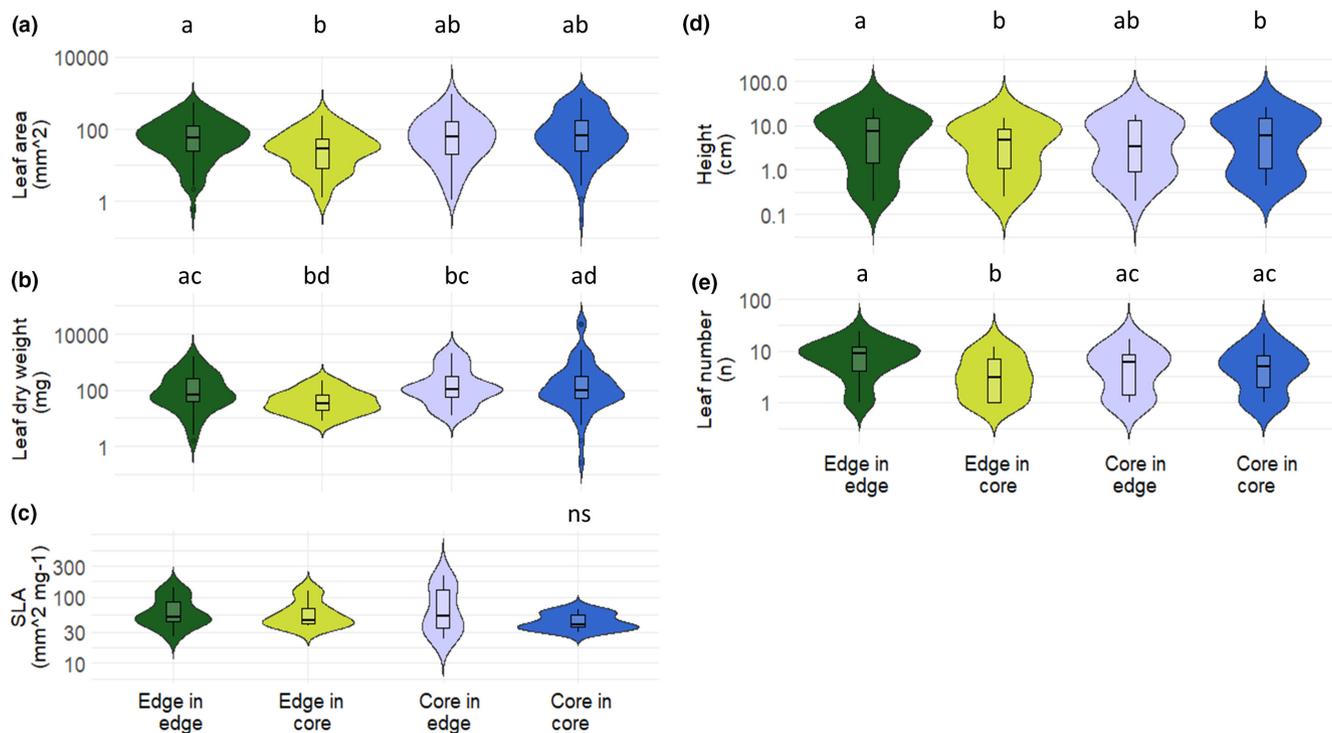
3.3 | Intra- versus interspecific trait variation

The observed variability in plant height and SLA was mostly caused by community compositional shifts (Table 3) with a positive covariation between turnover and intraspecific variability for plant height and a negative covariation for SLA. Variability in leaf number was instead mainly caused by ITV and to a lesser extent by species turnover or changes in species abundances (Table 3). Turnover and ITV had an opposite effect on leaf number variability (negative covariation −2.48, Table A7 in the Supporting Information), e.g. ITV was lower in seedling communities with more leaves, on average. Accounting for ITV increased the explanatory power of the fixed-effect variables in the models for the CWM of plant height (marginal R^2 of 0.38 vs 0.25, Table A7 in the Supporting Information) and CWM of leaf number (marginal R^2 of 0.29 vs 0.19, Table A7 in the Supporting Information). The translocation from high- to low-elevation forests caused intraspecific changes in CMW plant height whereas variations in SLA were more due to species turnover (Table A7 in the Supporting Information). Changes in CWM leaf number were due to both species turnover and ITV (Table A7 in the Supporting Information). Turnover was also responsible for changes in CWM SLA as well as for differences in CWM plant height between regions. Instead, the variation in leaf number between regions was more explained by intraspecific variation. Finally, ITV in CWM SLA was responsible for the observed variation between edge and core.

FIGURE 3 Violin plots showing variation in mean values of species trait (without species cover) from the realised soil seed bank at the forest edge vs core and after the translocation of the soil from the core to the edge and vice versa for (a) leaf area, (b) leaf dry weight, (c) specific leaf area (SLA), (d) plant height, (e) leaf number. The mean of leaf area, leaf dry weight and SLA were log-transformed for the analysis and back-transformed into the original scale for data visualisation. Significant differences (for $p < 0.05$) between groups are given by letters above the violin plots and refer to the models' results (Table 1; Table A5 in the Supporting Information for the 'core in core vs core in edge' comparison).

TABLE 1 Summary of the results of Linear Mixed-Effect Models and Generalized Linear Mixed Models using Template Model Builder (LMMs and glmmTMB respectively) for plant height, leaf area, leaf dry weight, specific leaf area (SLA) and leaf number [mean values of species trait (without species cover)] with the set of explanatory variables: edge vs core vs translocated soil ('edge soil in edge position' vs 'edge soil in core position' vs 'core soil in core position' vs 'core soil in edge position'); region (Belgium vs Italy); forest type (thinned vs unthinned) and elevation (high elevation vs low elevation vs high to low elevation vs low elevation).

	Intercept	Core in core	Edge in core	Core in edge	Italy (vs Belgium)	High to lowland (vs highland)	Lowland (vs highland)	Thinned forest (vs unthinned)	Edge in core: Italy	Core in edge: Italy	Core in core: Italy	R^2 marginal	R^2 conditional
Plant height	−0.87	−2.85↓**	−2.41↓**	−1.72	12.18↑***	8.19↑***	7.47↑*					0.15	0.66
Leaf area	−0.56	−0.03	−0.12↓*	0.03	0.41	0.48↑***	0.01	0.38↑**				0.08	0.73
Leaf dry weight	−3.49	−0.15	−0.16↓**	−0.05	0.90↑***	0.52↑***	0.14	0.33↑**				0.14	0.70
SLA	2.08	−0.07	−0.55↓**	0.32	−0.54↓***	−0.03	−0.14↓*					0.07	0.42
Leaf number	−0.42	−0.07			1.99↑***	0.39↑***	0.79↑***		0.22	−0.45↓*	−0.21	0.23	0.43

Note: The reference category for each variable is reported in parentheses. The comparison between 'core soil in core position' and 'core soil in edge position' was done by running the same set of models but changing the reference category (the result is shown in Appendix A5 in the Supporting Information). The direction of the effect is indicated by positive or negative estimates and upward or downward arrows. Empty cells indicate no significant effects. The significance of *p*-values is given as ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$. Model fit was assessed based on marginal R^2 (proportion of variance explained by fixed effects) and conditional R^2 (proportion of variance explained by both random and fixed effects; Nakagawa & Schielzeth, 2013).

3.4 | Species-level trait responses

Generally, specialists and generalists responded similarly to translocation from high- to low-elevation forests, with increased plant height and leaf number (e.g., *Alliaria petiolata* (M.Bieb.) Cavara & Grande, *Cardamine hirsuta*, *Carex sylvatica* Huds. and *Moehringia trinervia*) and decreased SLA (e.g., *Alliaria petiolata*, *Chaerophyllum temulum*, *Carpinus betulus* and *Digitalis lutea* subsp. *australis* (Ten.) Arcang.) (Table 2). Responses to the translocation from the edge to the core and vice versa differed among species: in the translocation from the core to the edge, height increased in the generalist *Cardamine hirsuta* while it decreased in the specialist *Luzula forsteri* (Table 2). In the translocation from the edge to the core, the number of leaves decreased in *Campanula rapunculus*, while plant height increased in *Chaerophyllum temulum* (Table 2). Finally, the leaf number increased after translocation from the core to the edge in the light-demanding species *Prunella vulgaris* (Table 2).

4 | DISCUSSION

4.1 | Trait responses to edge versus core microclimate

At the forest edge, higher temperatures and light availability enhanced plant growth through early germination and extended growing season, resulting in taller communities (Figure 3). The high proportion of generalist plants in the soil seed bank of forest edges and the competition between the seedlings due to increased plant cover (see also Gasperini et al., 2021) also contributed to this response. Soil seed bank communities at the edge include many open-forest species (Gasperini et al., 2022), which tend to have a physiological seed dormancy and germinate with light and warm temperatures (Blandino et al., 2022). These plants are usually tall and have a remarkable colonization capacity (Verheyen et al., 2003; Denelle et al., 2020; Blandino et al., 2022), since height is a major driver of seed dispersal ability (Thomson et al., 2018). Based on previous studies in European temperate forests (Chelli et al., 2019; Maes et al., 2020; Vanneste et al., 2020; Cubino et al., 2021), we also expected edges to be associated with more resource-conservative leaf traits in the understorey plants, such as a lower SLA; however, this was not confirmed since the translocation from the forest core to the edge resulted in only weak responses. Instead, stronger responses occurred with the translocation from the forest edge to the core. The shadier habitat of the forest interior decreased the growth and leaf production of the seedling community, likely as a result of the high proportion of light-demanding species in the edge soil which failed to thrive under limited light availability. Shade-intolerant species show high mortality (see also Gasperini et al., 2021) and strong growth constraints under low light conditions (Kobe et al., 1995). On the contrary, many shade-tolerant herbs of dense forests (Tinya et al., 2009) can respond positively to increased light availability (Tinya & Ódor, 2016), though with less
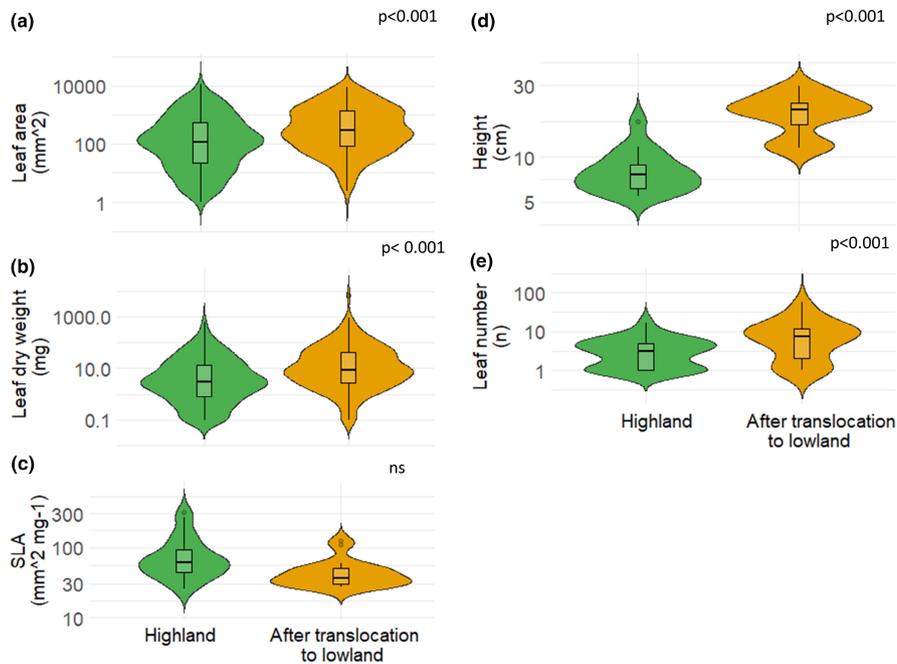
FIGURE 4 Violin plots showing variation in mean values of species trait (without species cover) from the realised soil seed bank at the high elevation, vs after the translocation of the soil to the low elevation, for (a) leaf area, (b) leaf dry weight, (c) specific leaf area (SLA), (d) plant height, (e) leaf number. The mean of leaf area, leaf dry weight and SLA were log-transformed for the analysis and back-transformed into the original scale for data visualisation. The significance of *p-values* is given as ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; and refers to the models' results (Table 1).

pronounced responses (i.e., of lower magnitude) than those of light-demanding species due to their weak competitive ability (Plue & Cousins, 2013).

The observed differences in mean trait values between the realised communities at the forest edge vs core are in contrast with recent findings about the potential soil seed bank of European temperate forests along the same gradient (Gasperini et al., 2022). This discrepancy, however, could depend on the group of traits considered in the study as well as on the source of the values used for the analyses. When these are retrieved from databases and not measured, as in the present study, it is in fact not possible to account for ITV (Cordlandwehr et al., 2013). In our experiment, trait variation along the edge-to-core gradient was driven by a microclimatic filter acting on two mechanisms, ITV (when individuals of the same species grew taller) and, to a lesser extent, community shifts in species composition (e.g. higher proportion of tall species). Recent evidence suggests that this divergence is maintained in the herb layer mainly as a result of intraspecific responses to light availability (Govaert et al., n.d.).

4.2 | Trait responses to translocation from high- to low-elevation forests

With the translocation of soil from high- to low-elevation forests, we simulated different climate-warming scenarios (Gutiérrez et al., 2021), with a microclimatic temperature increase between 1 and 3°C. This experiment showed the increased impacts of drought at two stages, during the seed to seedling transition and the following seedling development, especially during the summer. These impacts were both direct effects of reduced precipitation and indirect effects of higher temperatures that increased the water deficit in both soil and air. From late winter to spring, the warmer climate of low-elevation forests led to the development of taller seedling

communities (Figure 4), which is in line with evidence that plant stature increases with temperature (Moles et al., 2009; Govaert et al., 2021; Gasperini et al., 2022). This stimulating effect, however, takes place only as long as water is not a limiting factor, as plant stature generally decreases under more arid conditions (Gross et al., 2013; De la Riva et al., 2018). Moreover, the translocation from high- to lowland caused an increase in leaf area due to warm temperatures (Appendix A3 in the Supporting Information), followed by a stronger increase in leaf dry mass caused by water limitation starting from the late spring. This resulted in a slight decrease in SLA (Figure 4), and thus in the triggering of a more resource-conservative strategy. A similar pattern was also observed by Vangansbeke et al. (2022) in an experimental study on seedlings of forest herbs, where warming during the winter initially increased plant height, but then had no effect when kept constant during the growing season. In our study, as the season progressed towards the summer, the juvenile plants likely stopped growing in height and shifted to the production and investment of dry matter for adjusting their leaf traits to more arid conditions. Our leaf sampling was in fact done in July, when individual seedlings had already adjusted their SLA via increased production of dry matter for the construction of cell walls against incoming aridity (see for instance Niinemets, 2001 and Poorter et al., 2009).

Especially in the Mediterranean area and at lower altitudes, plants were exposed to prolonged summer drought stress and required specific adaptations to survive. Due to climate change, Italy is among the European countries that are most prone to extreme drought events and temperature increase (Rogora et al., 2018; Spinoni et al., 2018), with potentially severe impacts on vegetation (Pollastrini et al., 2019; Balzan et al., 2020). The lower mean SLA observed in Italy compared to Belgium was the result of a lower mean leaf dry weight as an adaptive adjustment to aridity. This adaptation is likely less important in the mesophilous forests of Belgium, where precipitation is more evenly distributed throughout the year. However, increasingly intense

TABLE 2 Values of plant height, leaf number and SLA correspond to the mean±standard deviation per species.

Taxon	Trait	Highland	High to lowland	Edge in edge	Edge in core	Core in edge	Core in core
Specialists							
Carex sylvatica Huds.	Plant height	3.21±1.47[a]	8.33±5.19[b]	—	—	—	—
	Leaf number	3.52±1.44[a]	4.33±0.71[b]	—	—	—	—
Carpinus betulus L	Leaf number	0.46±0.82[a]	1.54±1.13[b]	—	—	—	—
	SLA	68.98±27.70[a]	41.79±9.23[b]	—	—	—	—
Digitalis lutea subsp. australis (Ten.) Arcang.	Plant height	2.20±1.60[a]	10.25±8.61[b]	—	—	—	—
	SLA	113.79±108.05[a]	42.12±32.36[b]	—	—	—	—
Lactuca muralis (L.) E.Mey.	Plant height	15.34±10.06[a]	31.65±21.47[b]	—	—	—	—
	SLA	—	—	—	—	46.35±17.24[a]	86.18±82.43[b]
Luzula forsteri DC.	Plant height	—	—	10.85±5.93[ab]	7.47±3.10[a]	6.85±4.18[a]	12.56±4.33[b]
	Leaf number	—	—	8.80±3.79[b]	5.59±1.97[a]	9.54±5.24[b]	8.94±2.46[b]
Moehringia trinervia [Clairv.]	Plant height	1.21±2.36[a]	7.78±6.74[b]	—	—	—	—
	Leaf number	2.18±5.78[a]	24.78±21.45[b]	0.87±1.55[a]	0.52±1.07[a]	12.67±18.56[b]	9.33±12.39[b]
	SLA	72.38±35.04[a]	66.01±86.81[b]	—	—	—	—
Poa trivialis subsp. sylvicola (Guss.) H.Lindb.	Plant height	-	-	18±19.79[ab]	16±11.31[ab]	39.90±18.86[a]	4.25±2.63[b]
	Leaf number	-	-	32.50±38.89[ab]	5±4.24[ab]	16.10±6.97[a]	4.75±2.87[b]
Viola reichenbachiana Jord. ex Boreau	SLA	66.05±45.51[a]	31.51±8.17[b]	—	—	—	—
Generalists							
Alliaria petiolata (M.Bieb.) Cavara & Grande	Plant height	10.85±7.64[a]	25.50±5.15[b]	—	—	—	—
	Leaf number	2.27±0.90[a]	5.60±2.79[b]	—	—	—	—
	SLA	30.28±9.08[a]	12.18±7.05[b]	—	—	—	—
Campanula rapunculus L.	Plant height	5.20±2.93[a]	13.16±15.05[b]	—	—	—	—
	Leaf number	7±9.37[a]	—	3.40±1.81[a]	2.56±1.35[b]	3±1[ab]	2.67±0.58[ab]
Cardamine hirsuta L.	Plant height	—	18.82±12.61[b]	10.42±13.63[ab]	3.89±1.05[a]	18.05±11.27[b]	4.70±5.63[a]
	Leaf number	1.20±1.79[a]	21.09±11.88[b]	29.17±12.01[a]	21.67±5[a]	19.40±14.69[a]	4.80±5.02[b]
Carex flacca Schreb.	Plant height	7.31±3.35[a]	11.60±4.39[b]	—	—	—	—
Chaerophyllum temulum L.	Plant height	16.43±4.52[a]	27.81±8.99[b]	18.56±4.19[b]	27.82±8.19[b]	16.60±7.87[b]	23.80±13.72[ab]
	SLA	30.11±12.96[a]	19.84±9.75[b]	—	—	—	—
Clinopodium vulgare L.	SLA	—	—	39.48±9.4[b]	49.91±10.71[a]	38.66±15.31[b]	45.17±13.31[ab]

TABLE 2 (Continued)

Taxon	Trait	Highland	High to lowland	Edge in edge	Edge in core	Core in edge	Core in core
Cruciata glabra (L.) Opiz	Plant height	–	–	12.63±12.35[b]	32.75±11.29[a]	1±0[ab]	12.06±10.28[ab]
Erigeron canadensis L.	Plant height	–	–	37.29±27.87[ab]	28.92±27.89[ab]	39.11±18.97[a]	22.19±27.41[b]
	Leaf number	–	–	17.24±10.66[a]	15.08±14.52[ab]	18.33±8.38[a]	11.90±10.72[b]
	SLA	–	–	38.62±11.41[b]	53.16±30.74[a]	39.19±12.97[ab]	51.29±25.37[a]
Hypericum perforatum L.	Plant height	1.55±4.02[a]	12.25±12.79[b]	13.49±13.30[b]	5.28±7.93[ab]	6.62±7.28[ab]	2.09±3.14[a]
	Leaf number	2.53±5.35[a]	21.68±29.58[b]	26±32.81[a]	5.67±7.32[ab]	10.27±9.45[a]	1.71±2.93[b]
Inula conyzae (Griess.) Meikle	SLA	–	–	61.56±43.28[ab]	50.03±11.77[ab]	44.63±2.81[a]	98.25±54.54[b]
Poa trivialis L.	Plant height	11.13±11.11[a]	–	22.93±27.78[b]	11.92±26.01[a]	1.30±0.91[a]	6.35±12.43[ab]
Prunella vulgaris L.	Plant height	–	25.07±14.08[b]	17±0[a]	–	19.71±13.29[ab]	10.53±10.31[b]
	Leaf number	8.11±4.52[a]	17.20±8.93[b]	21±0	–	12.2±7.99[a]	7.74±4.54[b]
	SLA	50.48±22.94[a]	26.60±6.38[b]	–	–	–	–
Rubus fruticosus Lour.	Plant height	–	–	1.46±0.79[ab]	1.17±0.95[a]	2.37±1.86[b]	0.84±0.85[a]
Urtica dioica L.z	Plant height	–	–	4.97±3.38[b]	1.27±0.78[a]	4.67±7.22[ab]	0.50±0[a]
	Leaf number	–	–	6.73±2.24[b]	2.10±0.82[a]	8±1.73[b]	2±2.83[a]
Veronica officinalis L.	Plant height	–	–	1.39±1.49[b]	2.18±0.78[ab]	5.56±6.56[a]	6.69±9.04[a]
	Leaf number	–	–	1.86±3.29[b]	2.75±2.5[ab]	10.78±8.03[c]	8.89±10.82[ac]
	SLA	51.23±14.48[a]	19.66±6.41[b]	–	–	–	–

Note: The table shows the results of ANOVA followed by a post-hoc Tukey's honestly significant difference (HSD) test or a Kruskal–Wallis test followed by a Dunn's post-hoc test; depending on normality of the data distribution between treatments for a total of 24 species (those with a sufficient number of observations): eight forest herbs and 16 habitat generalists. Different letters show statistical significance at $p < 0.05$. –, data not available or not sufficient for statistical analysis.

TABLE 3 Decomposition of total variability for plant height, leaf number and SLA based on the sum of squares (between brackets) resulting from ANOVA on full models (Linear Mixed Models and Generalized Linear Mixed Models using Template Model Builder; LMMs and glmmTMB respectively) for the three traits.

	Turnover (CWM fixed)	Intraspecific variability (CWM itv)	Total variation (CWM specific)	Covariation
CWM Plant height	0.47 (6979.55)	0.19 (2733.33)	1 (14641.35)	0.34 (5028.47)
CWM Leaf number	0.62 (98.43)	2.87 (457.01)	1 (159.44)	−2.48 (−396)
CWM SLA	1.76 (5.31)	0.48 (1.44)	1 (3.01)	−1.24 (−3.74)

Note: Values represent the proportion of variability for each components (Turnover, ITV and Covariation) and were obtained by dividing the sum of squares resulting from the models by the total variability (CWM specific) for each trait (Lepš et al., 2011). Turnover stands for variation in CWMs based on one value per species (CWM fixed); intraspecific variability stands for the variation in CWM due to intraspecific variability (ITV) only. For total variability is meant the variation in CWM calculated including both intraspecific variation and species turnover (CWM specific).The higher the value the higher the relative contribution of the component (ITV or species turnover) on the total functional community. If covariation is 0 species turnover and ITV affect the CWM independently. Positive (or negative) covariation denote a positive (or negative) correlation between the two components.

Abbreviations: CWM, community-weighted mean; ITV, intraspecific trait variation.

drought events due to climate change may become more frequent even in regions with an oceanic climate (EEA, 2016). Thus, understanding the capacity of plants to overcome these climatic extremes and adapt to changing climatic conditions is of utmost importance. Our findings support previous evidence that plant height tends to diminish with latitude (Moles et al., 2009) and that species with higher SLA are better adapted to longer winters and can thus cope with shorter growing seasons (Gonzalo-Turpin & Hazard, 2009).

Overall, the forest structure also influenced the traits of the juvenile plants from the soil seed bank. Larger leaf area in thinned forests was likely a response to higher light availability, whereas increased leaf dry weight was probably a result of the drier conditions of open vs dense stands. Robust evidence exists that forests with dense canopies reduce maximum temperatures and the vapour pressure deficit more efficiently than open forests (Davis et al., 2019; De Frenne et al., 2019; Zellweger et al., 2019). Hence, forest management can play an important role in driving the functional composition of the understorey primarily by driving the responses from the soil seed bank. In the context of climate change, we suggest that the maintenance of cooler and shadier microclimates, and thus close tree canopies, will likely prevent rapid functional shifts of the understorey through the soil seed bank and help mitigate the negative effect of heat and drought on the juvenile plants from the seed bank.

4.3 | Inter- and intraspecific trait variation

Overall, intraspecific variation was significantly influenced by microclimate, suggesting the importance to account for such effects to improve predictions about plant communities' responses to environmental changes (Laughlin et al., 2012; Cadotte et al., 2015). Intraspecific variability was caused by plastic adjustments to differences in environmental conditions. For example, the lower SLA found in the shade-tolerant *Lactuca muralis* or in the generalist *Inula conyzae* at the forest edge was likely useful to limit water loss due to evapotranspiration, through the development of smaller and thicker leaves. This is indeed a common

strategy to cope with water stress in other species of drought-prone habitats (Garnier et al., 2019). Moreover, wide differences were detected between species in response to our different treatments, although these were not clearly associated with the two groups of forest specialists and generalists considered here. For example, the specialist *Veronica officinalis* and the generalists *Chaerophyllum temulum* and *Cruciata glabra* behaved in a similar way, being smaller at the edge and bigger inside the forest. Also, the generalist *Campanula rapunculus* and the specialist *Luzula forsteri* showed decreased leaf number after the translocation from the forest edge to the core.

Our results, however, may have been influenced by the limited number of observations that we could obtain for some forest specialists. Compared with generalists, species of this group are known to have stronger germination constraints and to form soil seed banks with lower seed densities (Plue, Colas, et al., 2017). Stronger responses in the specialists, especially in the highland to lowland translocation experiment, may have not been detected because of a strong microclimatic filter acting upstream on germination. Besides reducing the number of forest specialists (as observed in Gasperini et al., 2021), the lowland climatic conditions have likely favoured species with greater tolerance to temperature and drought stress. Indeed, many species among forest specialists (e.g. *Carex sylvatica*, *Digitalis lutea* L., *Moehringia trinervia* etc.) and generalists (e.g. *Alliaria petiolata*, *Chaerophyllum temulum*, *Hypericum perforatum* L., etc.) had similar trait environment responses (Table 2). Ultimately, the limited duration of our experiment (one growing season) may have influenced the results, given that the seeds of some forest specialists may need a longer time and higher requirements for germination (Verheyen et al., 2003; Jankowska-Blaszczuk & Daws, 2007).

5 | CONCLUSIONS

We showed significant shifts in inter- and intraspecific traits in the realised soil seed banks of temperate forests of two European

regions, along macro- and microclimatic gradients. Understorey plants at their early life stages were sensitive and plastic to environmental changes, and able to adjust their traits to climatic variations. This points to the importance of considering the establishment and development of seedlings when assessing plant responses to global changes. Trait responses of juvenile communities from the seed bank were altered along the edge-to-core gradient. We suggest that this may turn into changes in the functional composition of the understorey which are often associated with changes in ecosystem processes. Hence, the creation of new forest edges and fragmentation should be limited as much as possible, while large and continuous forest areas should be preserved to ensure the most favourable microclimatic conditions for the below-canopy biodiversity. Temperature increase that resulted from the high to low translocation led to increased plant height, number of leaves, leaf area and leaf dry weight, suggesting that warming could bring early functional shifts in the juvenile understorey from the seed bank, in a more resource-acquisitive direction. To mitigate these shifts, forest management practices which do not exacerbate the negative effects of climate change should be promoted. Practices which open up the canopy cover at large scale or that exceedingly reduce forest density should be avoided. Finally, our findings indicate how intraspecific plasticity is important for the plant species' ability to persist in variable conditions, underlining the need to consider this component when predicting the responses of plant communities in a changing world.

AUTHOR CONTRIBUTIONS

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at: https://figshare.com/s/cd75a3ee6e0af1ff9735.

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SUPPORTING INFORMATION

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

Appendix A1. Map showing the eight sites distributed in Italy and Belgium.

Appendix A2. Site descriptions.

Appendix A3. Summary of microclimatic soil and air temperatures per site.

Appendix A4. Overview of the community means response variable per region.

Appendix A5. Results for linear mixed-effects models (LMMs) and Generalized Linear Mixed Models using Template Model Builder (glmmTMB) showing core soil in core position vs core soil in edge position.

Appendix A6. Categorization of the species in forest guilds following Heinken et al. (2022).

Appendix A7. Linear mixed-effects models (LMMs) and Generalized Linear Mixed Models using Template Model Builder (glmmTMB) for community-weighted mean (CWM) plant height, specific leaf area (SLA) and leaf number.

Appendix A8. Complete list of species found in each site.

Appendix B1. Set of photographs of seedlings and young plants emerged from the soil seed bank.

Appendix B2. Set of photographs of seedlings and young plants emerged from the soil seed bank.