

RESEARCH ARTICLE

Above- and belowground drivers of intraspecific trait variability across subcontinental gradients for five ubiquitous forest plants in North America

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Abstract

1. Intraspecific trait variability (ITV) provides the material for species' adaptation to environmental changes. To advance our understanding of how ITV can contribute to species' adaptation to a wide range of environmental conditions, we studied five widespread understorey forest species exposed to both continental-scale climate gradients, and local soil and disturbance gradients. We investigated the environmental drivers of between-site leaf and root trait variation, and tested whether higher between-site ITV was associated with increased trait sensitivity to environmental variation (i.e. environmental fit).
2. We measured morphological (specific leaf area: SLA, specific root length: SRL) and chemical traits (Leaf and Root N, P, K, Mg, Ca) of five forest understorey vascular

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plant species at 78 sites across Canada. A total of 261 species-by-site combinations spanning ~4300 km were sampled, capturing important abiotic and biotic environmental gradients (neighbourhood composition, canopy structure, soil conditions, climate). We used multivariate and univariate linear mixed models to identify drivers of ITV and test the association of between-site ITV with environmental fit.

3. Between-site ITV of leaf traits was primarily driven by canopy structure and climate. Comparatively, environmental drivers explained only a small proportion of variability in root traits: these relationships were trait specific and included soil conditions (Root P), canopy structure (Root N) and neighbourhood composition (SRL, Root K). Between-site ITV was associated with increased environmental fit only for a minority of traits, primarily in response to climate (SLA, Leaf N, SRL).
4. *Synthesis.* By studying how ITV is structured along environmental gradients among species adapted to a wide range of conditions, we can begin to understand how individual species might respond to environmental change. Our results show that generalisable trait–environment relationships occur primarily aboveground, and only accounted for a small proportion of variability. For our group of species with broad ecological niches, variability in traits was only rarely associated with higher environmental fit, and primarily along climatic gradients. These results point to promising research avenues on the various ways in which trait variation can affect species' performance along different environmental gradients.

KEYWORDS

biotic interactions, canopy structure, climate gradient, edaphic conditions, environmental matching, functional ecology, phenotypic plasticity, tissue nutrient concentration

1 | INTRODUCTION

Functional traits, because of their effects on migration and demographic processes, have been proposed as one way to capture species' responses to global environmental change (Aubin et al., 2016; Berzaghi et al., 2020; Chardon et al., 2020). Specifically, intraspecific trait variability (ITV) is associated with species' coexistence across diversity gradients and is an important component of species' responses to environmental gradients (Benavides et al., 2019; Moran et al., 2016; Violle et al., 2012). Robust associations have been documented between well-studied aboveground traits and environmental gradients, such as light and precipitation (e.g. Midolo et al., 2019). In contrast, linkages between belowground traits and environmental gradients remain an open question, despite increasing interest in their relevance for species' responses to climate change (Hagedorn et al., 2019). Here, we address this knowledge gap by jointly investigating the biotic and abiotic drivers of both above- and belowground ITV in forest plants that occur over broad ecological gradients.

Forest plant community composition results from a series of abiotic and biotic filters (henceforth 'environmental') acting at different scales (Kraft et al., 2010), where ITV can influence ecological assembly. Environmental filtering operates not only via selection from a species pool, but also by selection of individuals within species (Ackerly, 2003; Shipley, 2010; Violle et al., 2012).

Because ITV provides the variation upon which filters can act, one might expect higher ITV to allow individual species to better cope with environmental conditions at the local scale (i.e. environmental matching) and therefore allow them to exploit broader niches (Ackerly, 2003). However, this is not necessarily the case. ITV can also be unstructured, that is, determined by non-spatial or random processes that impact species' responses to environmental change in other ways (Joner et al., 2012; Matesanz et al., 2010; Moran et al., 2016). For instance, *portfolio effects* manifest when trait variation stabilises species' performance in the face of environmental variability, but without providing a net adaptive advantage (Bolnick et al., 2011). One way to capture the effect of unstructured ITV on species' responses to these changes within predictive models is simply to introduce stochasticity in trait estimates (Matesanz et al., 2010; Moran et al., 2016). In contrast, for ITV that corresponds predictably to climate, soil conditions, canopy structure or competitive dynamics (neighbourhood composition), using the same procedure can vastly underestimate the effect of ITV, both on community assembly mechanisms and species' responses to environmental change (Moran et al., 2016; Violle et al., 2012). In this study, we investigate the strength and generality of above- and belowground intraspecific trait–environment relationships. We ask whether higher ITV is associated with higher environmental fit for widely distributed North American boreal and temperate

understorey plant species. The answer to these questions can help us understand how ITV may be involved in how these species achieve broad ecological niches.

It is well known that leaf morphological traits such as lamina thickness, area and nutrient concentrations respond plastically to the light environment in which a leaf develops (Poorter et al., 2019), and this extends to other aboveground traits (Burton et al., 2017; Lemke et al., 2015). At much larger spatial scales, variation in aboveground traits also shows consistent links with climatic factors such as precipitation and temperature (Midolo et al., 2019). These relationships have garnered much interest because of the role they might play in species' responses to environmental change. In contrast, belowground trait–environment relationships have received far less attention, but are increasingly recognised as an important component of species' individual responses to environmental change (Hagedorn et al., 2019). Early studies focusing on climatic and resource gradients (light, soil N) show primarily species-specific responses of root traits (Burton et al., 2017). But this has necessarily left out important sources of variability in soil conditions, like pH, with which roots may interact more directly and that are known to affect community-level traits (e.g. St. Martin & Mallik, 2021). It is therefore not known which environmental drivers structure ITV in root traits, and if they are the same as those that structure ITV in leaf traits.

In addition to abiotic factors, competitive neighbourhood effects that are internal to plant communities can also affect ITV within and between sites (HilleRisLambers et al., 2012). For instance, limiting similarity (Chesson, 2000) posits that interspecific competition should minimise niche overlap among coexisting species in a community (i.e. maximise differences; Benavides et al., 2019). Alternatively, competitive exclusion can select towards similarity in certain traits (HilleRisLambers et al., 2012). In both cases, competitive dynamics are expected to affect not only within-site ITV, but also site-level trait means, such that differences in intraspecific or interspecific competitive environment should result in more between-site variability than expected from differences in the abiotic environment alone. Several studies have shown that total plant cover, a proxy for competition, can explain some portion of between-site ITV for traits such as SLA, Leaf N concentration and plant height (Burton et al., 2017; Helsen et al., 2017; le Bagousse-Pinguet et al., 2015). In particular, pairwise differences in Leaf N and plant height are associated with competitive exclusion among species (Kraft et al., 2015), which can also lead to a reallocation of resources from roots to leaves and a shift towards smaller fine root diameters (Bennett et al., 2016). Although few studies have investigated this in situ, this is one mechanism through which linkages between above- and belowground processes could affect species' responses to environmental change.

The environmental matching hypothesis advances that species' niche breadth is the result of variation in traits that allow species to respond to variations in the environment by allowing them to find ('match') the local adaptive optima and achieve higher fitness at the local scale (Ackerly, 2003). In other words, ITV must (1) respond to environmental variation and (2) lead to increased local fitness. If ITV allows species to match their environment, we might predict

that higher ITV allows species to occupy broader ecological niches (Bolnick et al., 2011; Sides et al., 2014). However, a number of studies have shown inconsistent links between ecological niche breadth and ITV (Hermant et al., 2013; Mitchell et al., 2017; Sides et al., 2014; Treurnicht et al., 2020). Another way to approach the first part of this question is to compare the extent of between-site trait variation among species with similar niche breadth with some measure of how closely they respond to (or 'fit') environmental conditions (Mitchell et al., 2017). In North American temperate and boreal biomes, many widespread understorey plants occur along both continental-scale climatic gradients (temperature, precipitation), and in a wide range of soil conditions and natural disturbance regimes (fires, insect outbreaks, windthrow). As a result, many understorey plants can typically acclimate and reproduce in open sites where microclimate and community structure have been dramatically altered from the forested state (Gilliam & Roberts, 2003). If these species achieve broad ecological niche breadth via environmental matching, we expect to find increasingly better fit (higher R^2 value) between environmental conditions and site-level trait values as traits become more variable (higher trait coefficient of variation; CV; Figure 1).

In this study, we investigate the importance of local- and continental-scale biotic and abiotic environmental drivers on ITV of aboveground and belowground traits. To do this, we focus specifically on five widespread understorey forest species with broad ecological niches. The remarkable ability of these species to adapt to a range of environmental conditions presents a unique opportunity to investigate how ITV might be involved in their response to environmental variation, and whether there is any generality in how such species achieve their extensive environmental range. Specifically, we ask whether higher between-site ITV in the traits of these species is associated with increased environmental fit with the

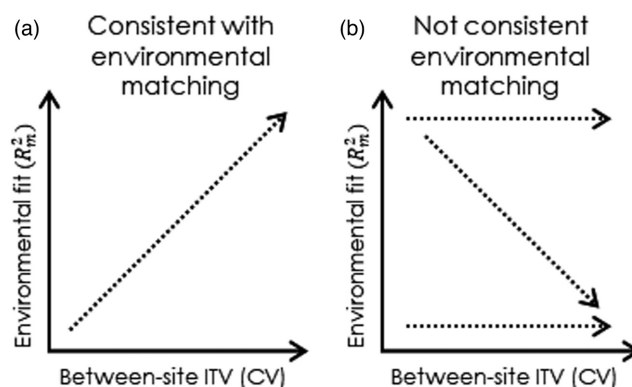


FIGURE 1 Predictions consistent with the environmental matching hypothesis. One way to test for patterns consistent or not with the environmental matching hypothesis is to ask whether traits that are more variable between sites also have a better fit with the environment for species with similar niche breadth (a). In contrast, negative or null slopes between intraspecific trait variability and environmental fit indicate that additional trait variation is not associated with increased environmental fit, either at the species or trait level, relative to a given environmental gradient (b)

broad biotic and abiotic gradients across which their ranges extend (Figure 1). To facilitate comparison, we use analogous aboveground and belowground morphological and chemical traits. First, we investigate multivariate and univariate drivers of between-site ITV. We predict that aboveground trait variability is primarily driven by climate, canopy structure (affecting light availability as well as microclimatic factors) and neighbourhood composition (reflecting the competitive environment). In contrast, we predict that belowground ITV is primarily driven by soil conditions. Second, we hypothesise that, among similarly widespread forest understorey plants, individual species' response to environmental variation is positively associated with their between-site variability. We therefore predict a positive relationship between species' trait CV and the fit of traits with important environmental gradients (following our first initial predictions). We test this hypothesis by modelling the relationship between species-level trait CV and environmental fit with each environmental driver category (neighbourhood composition, canopy structure, soil conditions, climate), and examining the partial slopes obtained from these models.

2 | MATERIALS AND METHODS

The study was conducted as part of the CoVITAS project (Aubin et al., 2020), a collaborative science initiative involving 23 research teams across Canada (Table A.1, Supplementary Material). This study focuses on a subset of species and sites from this original dataset to

address specific questions about environmental drivers of ITV and trait–environment relationships (Kumordzi et al., 2019; described in Appendix A, Supplementary Material).

2.1 | Study area and focal species

Our study focused on five ubiquitous understorey species that occur across deciduous, mixed and coniferous forests in temperate and boreal regions of Canada (Figure A.1, Supplementary Material; Kumordzi et al., 2019). This includes one shrub, *Vaccinium angustifolium* (Ericaceae; VAAN), and four forbs: *Maianthemum canadense* (Asparagaceae; MACA), *Trientalis borealis* (syn. *Lysimachia borealis*, Primulaceae; TRBO), *Aralia nudicaulis* (Araliaceae; ARNU) and *Cornus canadensis* (Cornaceae; COCA, which has a woody base but forb-like growth habits). Despite being similarly widespread, these species show different magnitudes of trait variability, and this variability is structured differently above- and belowground and across spatial scales (Kumordzi et al., 2019). These species also vary in their growth habits, forming either dense colonies (VAAN), semi-dense populations (MACA, COCA, ARNU) or growing only sparsely (TRBO).

The study area forms a subcontinental belt ~4300 km long spanning the Canadian provinces of Alberta in the west to Newfoundland in the east, and from 56.80°N latitude in northern Alberta to 45.20°N latitude in southern Québec (Figure 2). The study area is characterised by strong subcontinental variation in temperature (negatively correlated with latitude) and precipitation (generally decreasing

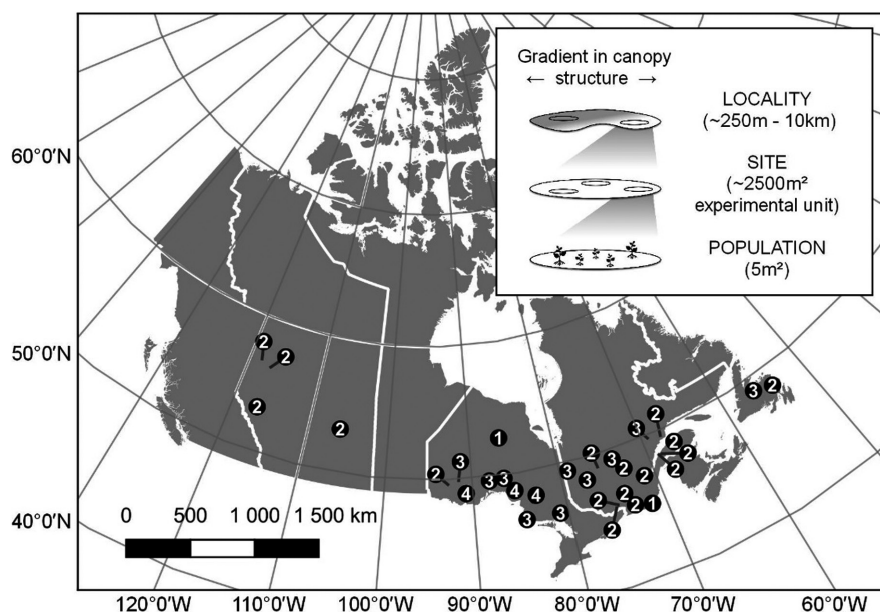


FIGURE 2 Study area and sampling design. Sampling sites (78) spanned from Newfoundland in the east to Alberta in the west, and the latitudinal breadth of the mixed and boreal forest in Canada. To facilitate sampling, sites were clustered within 32 localities, where 1 to 4 sites spanning a range of canopy structures were selected (number of sites per locality indicated as a circled number). To obtain site-level trait averages for each species (the scale of interest in the present study; see map inset), we sampled three populations of each focal species that was present and aggregated these values, for a total of 261 species-by-site combinations. All analyses were carried out on all species' site-level values, and accounting for the non-independence of sites clustered within a given locality. Further details on site locations and environmental gradients are provided in Table A.1, Table A.2 and Figure A.2 (Supplementary Material)

from east to west). Growing degree days (Heat sum $>5^{\circ}\text{C}$; $\text{GDD}_{>5}$) varied across sites from 895 to 2094 and total annual precipitation from 424 mm to 1467 mm. The study area is also characterised by substantial variation in soil types due to underlying variation in geological formations and surface deposits (e.g. Interior Plains, Canadian Shield, Clay belt), as well as variation in topography and climate (Bone, 2018). Following broad climatic gradients, disturbances also vary in frequency and intensity, including fire, insect outbreaks (e.g. *Dendroctonus ponderosae* in the west, and *Choristoneura fumiferana*, in the east), as well as logging and silvicultural activities (Natural Resources Canada, 2020).

Our focal species co-occur across these environmental gradients, including different canopy structures (from open to closed, as a result of disturbance), composition (deciduous, mixed or coniferous) and soil conditions (nutrient rich to poor; see Table A.2 and Figure A.2 for environmental amplitude covered by each focal species, Supplementary Material).

2.2 | Study design

In all, 23 field teams sampled focal species from 78 sites across the study area following a standardised protocol, with samples subsequently centralised for further analyses by core laboratories. Sites were selected to capture the full ecological niche breadth of the focal species and characterised in terms of dominant climatic, soil and disturbance gradients. This resulted in 261 species-by-site combinations. Study sites ($\sim 2500\text{m}^2$) with different disturbance histories, including a range of understorey and canopy conditions, were nested within 32 localities ($\sim 250\text{m}$ – 10 km ; Figure 2). Disturbance types included fire, insect outbreaks, various silvicultural harvesting practices, as well as Ni-Cu smelter deposition. Disturbances contributed to more open canopies, and thus increased light availability and evapotranspiration compared to undisturbed sites. While this study does not focus on the effects of disturbance types per se, this experimental design allowed us to capture the full range of canopy conditions typically generated by these disturbances, and thus to draw general conclusions about environmental gradients associated with disturbance regime. All sampling and in situ measurements were carried out between July 10th and 25th, 2014. No permits were required to conduct fieldwork.

2.3 | Trait measurements

For each focal species present at a site, we collected root and leaf material from three populations (i.e. ramets and/or individual plants located within a homogeneous 5 m^2 area) located approximately 50 m apart. In a few cases where the focal species was sparse, fewer than three populations were sampled. We harvested 10 to 30 fully mature leaves from 3 to 5 individuals in each sampled population, for which we recorded fresh leaf area using scanners and cameras. Once dried, leaves were sent to a central location for processing, weighing and grinding (20-mesh screen using a Wiley mill). Tissue digestion was

conducted with H_2SO_4 – H_2O_2 . Nutrient concentrations were measured by spectrophotometry (FIA Quickchem, Lachat) and inductively coupled plasma analysis (ICAP-9000, Thermo Instruments). We assessed leaf tissue concentrations for N, P, K, Mg and Ca. Leaf area and dry weight were used to obtain SLA.

The root system of 3 to 5 individuals per population was carefully excavated to ensure the collection of at least 10 absorbing fine roots in good condition. Samples were packaged in wet and cool conditions and shipped to a central location for processing. First-order fine roots were identified in the laboratory based on the presence of root caps and were then measured, dried and weighed to obtain specific root length (SRL). These roots were subsequently ground and analysed for nutrient content, including N, P, K, Mg and Ca concentrations following the same procedure as above. For further details on trait measurements, sample processing and chemical analyses, see Kumordzi et al. (2019).

Population-level leaf and root trait values were pooled to the site level for each species. Therefore, the values analysed from this point forward represent an average of the populations sampled at each site and for each species, containing no information on within-site variability.

2.4 | Environmental gradients

We focused on 11 environmental gradients grouped into four categories of biotic and abiotic environmental drivers of ITV that reflect the primary sources of environmental heterogeneity experienced by species in our forested systems: neighbourhood composition, canopy structure, soil conditions and (macro)climate (Table 1).

Neighbourhood composition, that is, the composition of the understorey community, was estimated in three separate $5 \times 5\text{ m}$ quadrats for each site. Quadrats were placed in the immediate neighbourhood of the focal species population, except in a few cases where the focal population was sparse and required additional sampling outside the plot. This allowed us to sample the range of densities in which our focal species are typically found (Table A.2, Figure A.2). Within these quadrats, each species with a percent cover greater than 5% was recorded and attributed a percent cover class (2: 6%–25%, 3: 26%–50%, 4: 51%–75%, 5: 76%–100%). Focal species measured at a site but with a cover under 5% were noted and attributed a cover class of <5%. These observations were aggregated to obtain site-level understorey composition. We used cumulative understorey species cover ($\text{Cover}_{\text{Tot}}$) and percent cover of the focal species ($\text{Cover}_{\text{Foc}}$) to capture differences in interspecific and intraspecific competitive environment.

Competitive dynamics can also be characterised by the amount of functional overlap among interacting species. We focused on three key traits that capture important resource investment trade-offs and affect plant competitive abilities: SLA, maximum height and seed weight (Westoby, 1998). Species' average values were obtained from the TOPIC database for focal and co-occurring species (Aubin et al., 2020), accounting for all recorded species. We used the FDis metric of Laliberté et al. (2010) to capture functional

TABLE 1 Environmental drivers and variables. Summary of environmental gradients investigated in this study, grouped by category of environmental driver. Abbreviations provided here are used throughout the text

Environmental driver	Variable	Type	Unit	Abbreviation
Neighbourhood	Functional dispersion	Continuous	(unitless)	FD
	Percent cover of focal species	Continuous	%	Cover _{Foc}
	Cumulative relative cover	Continuous	Cumul. %	Cover _{Tot}
Canopy structure	Live basal area	Continuous	m ² ha ⁻¹	BA
	Coniferous (>25% of stand BA)	Binary factor	0;1	Conifer
	Deciduous (>25% of stand BA)	Binary factor	0;1	Deciduous
Soil conditions	Drainage class	Ordered factor	1 to 7	Drainage
	Soil pH	Continuous	Log[H ⁺]	Soil pH
	Organic layer depth	Continuous	cm	Humus depth
Climate	Growing degree days above 5°C	Continuous	GDD	GDD _{>5}
	Mean annual precipitation	Continuous	mm	MAP

dispersion of each neighbourhood community. FDis represents the abundance-weighted mean distance of species in a community to the abundance-weighted centroid of that community. Because it is based on species' mean traits and not on site-level measurements, the resulting metric remains an approximation of the true FDis at each site, but it allows us to establish a comparison among strongly contrasted sites (coded 'FD' henceforth).

Canopy structure, defined here as the general attributes of the tree layer affecting understorey environmental conditions, captured environmental gradients associated with disturbance history and stand type. We identified and measured all living trees (>9 cm diameter at breast height, defined as 1.3 m) within an 11.3 m radius (0.04 ha) at each study site, and used live tree basal area (m² ha⁻¹, BA) as a proxy for light and microclimate effects. We used two binary variables to capture broad differences in stand composition, where 1 denoted that coniferous or deciduous species represented >25% of total stand basal area (mixed stands were assigned 1 for both variables). To ensure that these categories represented biologically meaningful differences, sites with <1 m² ha⁻¹ total basal area were assigned 0 for both variables.

Soil conditions. Several important edaphic gradients typically structure vegetation communities in these forests. For each study site, field teams first estimated drainage class (7 categories from 'excessive drainage' to 'very poor drainage'; Saucier et al., 1994). We then dug one 30×30 cm soil pit to measure humus depth (cm), that is, residual organic matter at varying degrees of decomposition on top of the mineral soil layer. Finally, one mineral soil sample per site was collected at a depth of 30 cm (horizon B or C, depending on site) and soil pH was measured in 0.01 M CaCl₂ in a 2:1 volume mixture.

Macroclimate (henceforth referred to as climate). The dominant climatic gradients present at the subcontinental scale in these forests are temperature (north–south) and precipitation (east–west). For each locality, we obtained the number of growing degree days above 5 °C (GDD_{>5}) and total annual precipitation (in mm, MAP) averaged over a 30-year period (1985–2014), as based on the interpolated climate data from the BioSIM model (Régnière et al., 2014).

2.5 | Statistical analyses

We used a linear mixed model approach to first (1) investigate generalisable intraspecific trait–environment relationships (for leaf and root traits by group, then for each trait individually), and then (2) to assess the association between ITV and environment fit at the species' trait level. All analyses were carried out in R version 3.5.2 (R Core Team, 2018). Our 11 environmental gradients, divided into four categories of drivers (Table 1), showed no excessive correlations (Variance Inflation Factor, VIF < 4; see also Figure A.3, Supplementary Material), and were centred and scaled prior to all analyses (with the exception of binary variables). Both traits and environmental drivers were transformed as needed to improve the symmetry of distribution.

2.5.1 | Environmental drivers of ITV

Because they can account for structured survey designs and species identity, individual trait–environment relationships are often characterised using linear mixed models (Burton et al., 2017; Helsen et al., 2017; Weemstra et al., 2021). Here, one major additional question is the extent to which leaf traits and root traits respond to the same environmental drivers: that is, we wished to describe two multivariate trait–environment relationships, one for leaf traits (SLA and Leaf N, P, K, Mg, Ca) and one for root traits (SRL and Root N, P, K, Mg, Ca), accounting for survey structure and species effects. We used linear mixed models to fit all possible combinations of our four environmental drivers (neighbourhood, canopy structure, soil conditions and climate) as fixed effects to characterise multivariate (grouped by leaf traits and root traits) and univariate (i.e. one trait at a time, 12 in total) trait–environment relationships.

Multivariate model set-up. To jointly model the best environmental predictors for a group of traits, we can verticalise the classic 'horizontal' trait dataset (where each trait is a column), and thereafter treat all trait values of a given species at a given site as repeated measurements of the same sampling unit, where each measurement

is coded by the new categorical variable 'Trait ID' (for an example with leaf traits, see Bernier-Cardou et al., 2016; for methodological notes, see Howell, 2016). Because different traits come in different units, values must first be centred and scaled for each trait. We then introduce Trait ID into the model, first as a fixed effect interacting with all environmental predictors, and second as a random slope for each random factor, causing the model to estimate the residual trait variance-covariance matrix among each level of these factors (Dworkin & Bolker, 2021; See Table B.1 for explicit model formulation). Finally, we remove the intercept of the model to focus on variation within traits, and not differences between traits (Dworkin & Bolker, 2021; see Table B.1, Supplementary Material).

To model how species' site-level traits vary across the full breadth of our sampled gradients, we also accounted for two potential sources of systematic differences among trait measurements. Because species can vary widely in their mean trait values, we accounted for 'species identity' by including it as a random term in our model. To account for any non-independence generated by our sampling design, variation that could be explained by 'locality' and 'site' effects nested within 'locality' was captured by two additional random terms. At this stage, we plotted estimates for each level of the nested 'site' effect using function qqmath from package lattice (Sarkar et al., 2018). Based on confidence intervals, estimates were not different from the mean and we excluded 'site' from our random effect structure from this point on. The final random structure of the model thus included 'species identity' and 'locality' effects, in addition to the Trait ID effect mentioned previously (see Table B.1). In contrast with univariate mixed models or classic multivariate approaches (e.g. Legendre & Legendre, 2012), our final model thus reflects the extent to which environmental variables can explain the multivariate variability of each species' traits while still accounting for survey structure.

Univariate model set-up. We followed the same rationale to model individual (univariate) trait-environment relationships. With no need to account for Trait ID or suppress the intercept when traits are analysed one at a time, we included more simply 'species identity' and 'locality' as crossed random effects, accounting for our study structure and the resulting non-independence among values (random intercepts, see Table B.1).

Model fit. For both types of relationship, we fitted models with all possible combinations of our four environmental driver categories as well as one null model, yielding 16 candidate models (models 1–16, Table B.1). Models were fitted based on maximum likelihood estimators using the lmer function from the lme4 (Bates et al., 2017). Following Burnham and Anderson (2002), model assumptions were verified for the full model (i.e. including all environmental drivers). To verify whether our results were robust to the inclusion of random slopes, we re-fitted each first-order model, allowing the response of each species to vary for each environmental gradient (models 1–4 in Table B.1, results in Figure B.1, Supplementary Material). To identify the most parsimonious ('best') model among the 16 candidate models, we selected the model with the lowest AIC_c value, as calculated using the aictab function from the AICcmodavg package (Mazerolle, 2020).

Model statistics. We estimated the conditional (R^2_c) and marginal R^2 (R^2_m) for each candidate multivariate model using the r.squaredGLMM function from the MuMIn package (Barton, 2020), to estimate effect size in mixed models (Nakagawa & Schielzeth, 2013). These R^2_m values were used to obtain the proportion of variance explained by each environmental driver (or combination thereof). The residual variance-covariance matrix of traits for root and leaf traits were obtained from both the full and the best multivariate model fits using the VarCorr function from package lme4 (Table B.3 Supplementary Material). Finally, we used the r2beta function of the r2glmm package to assess the size of individual fixed effects based on their semi-partial R^2_m (Jaeger, 2017). This is straightforward in univariate models, but in the multivariate models that lack an intercept, some adjustment to the model fit is required. To do this, we obtained the residuals from the null model (model 16, Table B.1) and fitted the multivariate model of interest (intercept, covariates and random effects) to the residuals of this null model. This preserved the variance structure of the original fit and forced r2beta to assess its fixed effects against the appropriate null model.

2.5.2 | ITV association with environmental fit

In a two-step modelling procedure, we used R^2_m as a measure of 'fit' between each trait of each species and environmental drivers (Mitchell et al., 2017), and compared it to the coefficient of variation (CV) of that trait. First, for each trait of each species, we fitted four linear mixed effects models with each category of environmental driver as fixed effects (i.e. neighbourhood, canopy structure, soil conditions and climate). These models thus describe all 12 trait-environment relationships for each species across all sites where that species was sampled (60 species-by-trait combinations, across 4 environmental gradients, for a total 240 models). As above, these models included a random component accounting for the non-independence of measurements from the same 'Locality' (Figure 2), and were fitted using restricted maximum likelihood estimators (REML; see Table C.1 for full model specification, Supplementary Material). Model assumptions were verified visually for each of the 240 models (homogeneity of variance, distribution of residuals), and models that did not conform were excluded from further visualisations ($n = 5$, out of 240). We used the r.squaredGLMM function from the MuMIn package (Barton, 2020) to estimate R^2_m for each model and thus obtain a measure of environmental fit.

Second, to test our specific hypothesis, these R^2_m values then became the response variable in a new model that captured the relationship between trait CV and R^2_m . To this end, we fitted a mixed model for each category of environmental driver, using trait ID and species ID as random effects to account for the non-independence of values in our sample (see Table C.1 for full model specification). These models were pooled by species and by trait, extracting the slope and intercept from these partial models. We used the bootMer function from the lme4 package to generate 95% and 90% confidence intervals around each slope estimate (2000 simulations). Slopes were considered positive if the lower bound was above 0.

3 | RESULTS

3.1 | Environmental drivers of ITV

Environmental variables considered in our study explained twice as much common variance among leaf traits ($R_m^2 = 0.115$, Figure 3a) than among root traits ($R_m^2 = 0.06$, Figure 3b). In both cases, a large proportion of the variance was captured by the combination of fixed and random effects (R_c^2 of 0.67 and 0.72, respectively, Figure 3), which included locality, species identity and trait identity. For leaves,

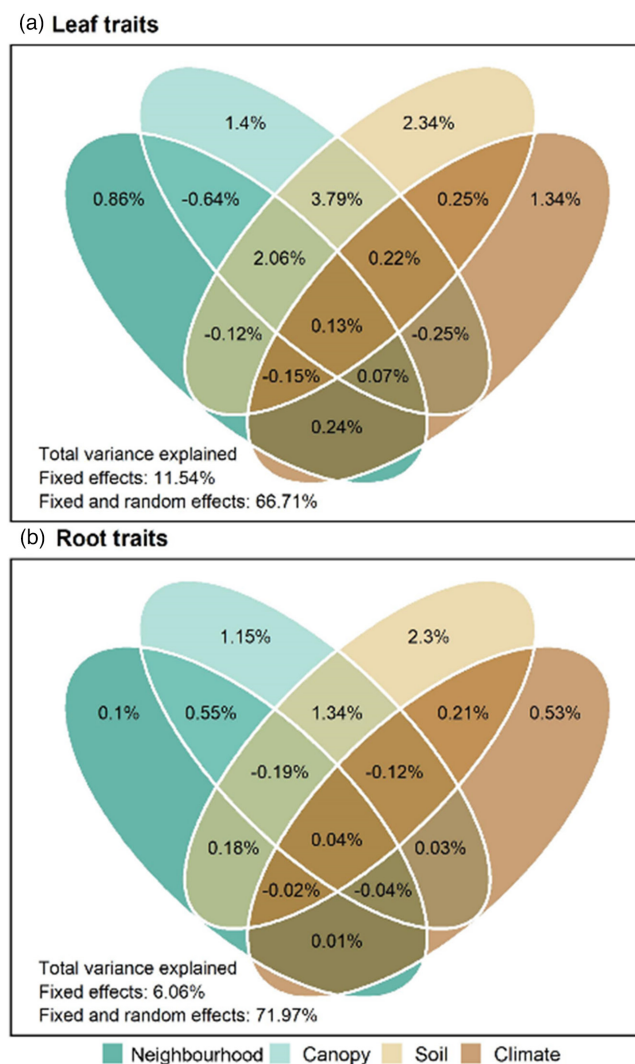


FIGURE 3 Multivariate variance partitioning. Proportion of total between-site variance captured by each category (or combination) of environmental variables for (a) leaf and (b) root traits of five widespread understorey species: *Aralia nudicaulis*, *Cornus canadensis*, *Maianthemum canadense*, *Trientalis borealis* and *Vaccinium angustifolium*. Proportion of between-site variance explained by each combination of fixed effects (R_m^2) and total variance captured by fixed and random effects together (R_c^2) are expressed as a proportion of total variance (%). Small negative values should be interpreted as 0. The random structure of the model includes species identity and locality, as well as Trait ID. See Table 1 for list of environmental variables included in each category

most of the common between-site variance within traits was captured by differences in canopy structure and climate (Figure 4a; see also Table B.2 and B.3, Supplementary Material). For roots, common variation was low and largely explained by soil variables (Figure 3), but the null model was the most parsimonious (Figure 4a).

At the trait level, fixed effects explained only a modest portion of variation among site-level trait values, with SLA and Root P demonstrating the highest fit (R_m^2 of 0.24 and 0.13 respectively, Figure 4a; see also Table B.4, Supplementary Material). Variation in Leaf N, K and Mg concentration was associated with canopy structure, and Leaf P and Mg were associated with climate gradients (Figure 4b). For leaf traits associated with canopy structure, their relationship was positively related to basal area, and (in most cases) negatively related to coniferous and deciduous overstory. Leaf P and Leaf Mg were both negatively related to $GDD_{>5}$, but showed opposite relationships to MAP. The best model that explained between-site differences in SLA was the only one to include neighbourhood composition (capturing competitive dynamics) and canopy structure, with SLA responding positively to FD and $Cover_{Tot}$, but negatively to $Cover_{Foc}$. For Leaf Ca, the intercept-only model was the best one. Across leaf traits, basal area had comparatively higher effect sizes than other predictors, particularly for SLA (semi-partial R_m^2 of 0.09, Figure 4b). In comparison, climate and neighbourhood variables had low semi-partial R^2 for all traits for which they were selected.

Among the root traits that were structured by environmental factors, SRL and Root K were best predicted by a combination of neighbourhood composition variables, but with relatively low effect size (Figure 4b). SRL and Root K both showed negative relationships with FD and positive relationships with $Cover_{Foc}$, but they had opposite responses to $Cover_{Tot}$. Root N was most closely associated with canopy structure and, despite low effect size, followed similar trends as Leaf N. Root P was the only individual root trait best predicted by soil variables. In this case, drainage class had a comparatively higher semi-partial R_m^2 (0.13, Figure 4b), with root P decreasing in sites with poorer drainage. Root P also decreased relative to soil pH, but increased relative to humus depth. The null model was the most parsimonious for two out of six individual root traits (Root Ca, Mg).

3.2 | ITV association with environmental fit

Environmental fit, measured here as the R_m^2 between the site-level traits of individual widespread understorey species and neighbourhood, canopy, soil and climate gradients, ranged from 0 to 0.54 (*A. nudicaulis* Leaf P relative to soil gradients, Table C.2). When we modelled the relationship of this environmental fit relative to trait between-site CV, we found a positive relationship between these two variables in the case of climate gradients for both leaf (SLA, Leaf N) and root traits (SRL; Figure 5a). For other environmental drivers, leaf trait between-site ITV was not associated with improved environmental fit (partial slopes were not greater than 0 based on 90% CI). Among root traits, Root K was the only other trait where higher

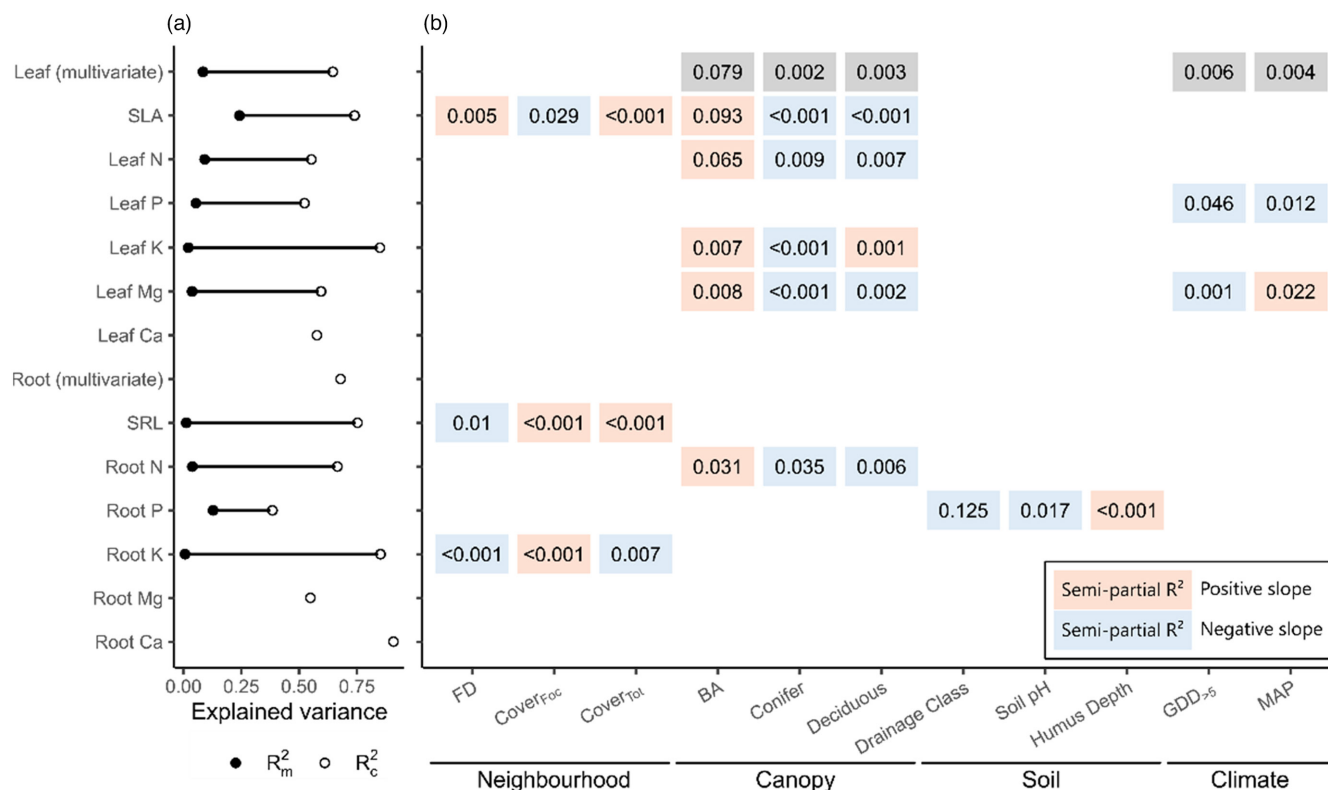


FIGURE 4 Environmental drivers of intraspecific trait variability. Best linear mixed model for predicting multivariate and univariate between-site variation in traits of five widespread understorey species: *Aralia nudicaulis*, *Cornus canadensis*, *Maianthemum canadense*, *Trientalis borealis* and *Vaccinium angustifolium*. Figure shows (a) overall model fit, captured by R_m^2 (●) and R_c^2 (○). Only R_c^2 is shown where the most parsimonious model was the null model. Semi-partial R^2 provides an indication of effect size for each fixed effect in the final model (b). Tile shade reflects the directionality, based on the sign of the estimated coefficients (red: positive; blue: negative). Multivariate models included random slopes, and therefore traits do not share a directionality (grey tiles). See Table 1 for abbreviations

between-site variation was associated with improved fit relative to differences in neighbourhood composition (Figure 5a).

For species, increased between-site trait variability was not associated with improved environmental fit relative to neighbourhood, canopy or soil conditions. Trait variability of *V. angustifolium* (VAAN) and *A. nudicaulis* (ARNU) showed positive relationships with environmental fit relative to climatic gradients (within a 95% CI, Figure 5b), but this was not the case for our other three study species: *C. canadensis* (COCA), *M. canadense* (MACA) and *T. borealis* (TRBO).

4 | DISCUSSION

We investigated the environmental drivers of aboveground and belowground ITV in five widespread understorey plants in North America. Then, we tested whether between-site ITV was positively associated with increased environmental fit at the species level, the first of two conditions for environmental matching. Our results show general drivers of aboveground ITV, including climate and (more strongly) canopy structure. No common driver of root ITV emerged, and traits were instead individually associated with soil conditions, neighbourhood and canopy structure. We found that between-site

ITV was positively associated with environmental fit in a minority of traits and species, primarily in response to climate, both for aboveground (SLA, Leaf N) and belowground traits (SRL). These results show that generalisable trait–environment relationships occur primarily aboveground and only account for a small proportion of variability. Most importantly, when we looked individually at our small set of broadly distributed species, although some traits of some species demonstrated high environmental fit, more variability in traits was only rarely associated with higher environmental fit. When this occurred, it was primarily in response to climate, raising the possibility that ITV plays different roles in species' responses to different environmental gradients across their ecological niche. We discuss these results, their limitations and avenues for further research towards a better understanding of how ITV contributes to species' response to environmental gradients.

4.1 | Environmental drivers of ITV

4.1.1 | Leaf traits

Our results were consistent with the expected response of leaf traits to light availability driven by canopy closure, both across traits

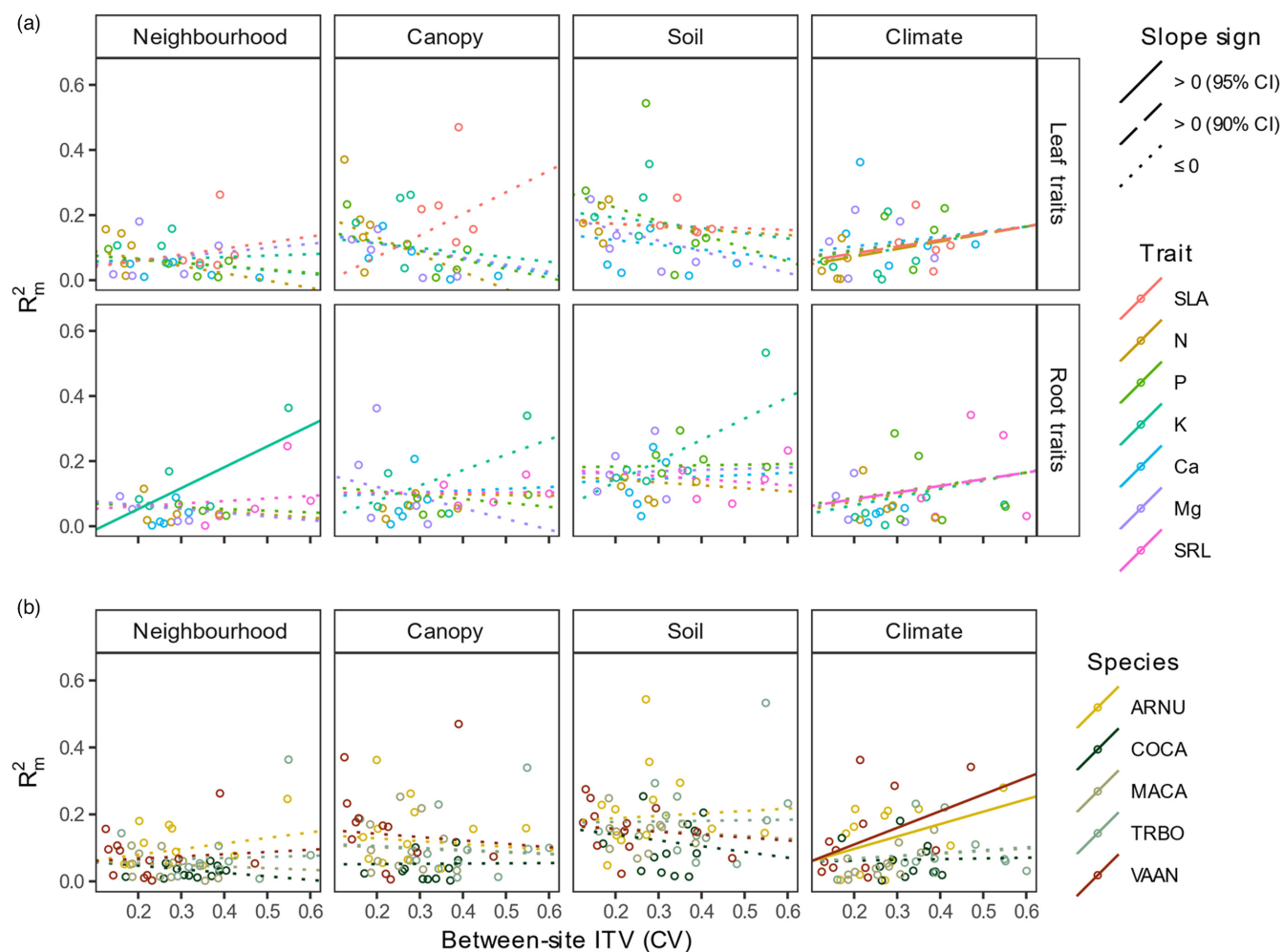


FIGURE 5 Intraspecific trait variability contribution to environmental fit. Plots show the proportion of species' between-site trait variation explained by each group of environmental predictors (R^2_m , y-axis) relative to the coefficient of variation (CV) of that trait (x-axis). To obtain R^2_m , four mixed models were fit with each of the four categories of environmental predictors as fixed effects and each trait of each species as the response variable. Each plotted point thus represents one of 60 species-by-trait combinations (5 species \times 12 traits). The overall relationship between the R^2_m and trait CV was modelled using a linear mixed model, allowing for random intercept and slope of species and trait effects. Panels show this modelled relationship partially pooled at the trait level (a), and at the species level (b). Solid and dashed lines show partial slopes that were above 0, based on 95% and 90% CI, respectively. Dotted lines show partial slopes that were not greater than zero. Species include *Aralia nudicaulis* (ARNU), *Cornus canadensis* (COCA), *Maianthemum canadense* (MACA), *Trientalis borealis* (TRBO) and *Vaccinium angustifolium* (VAAN). See Table 1 for other abbreviations. Plotted values are reported in Table C.2 (Supplementary Material)

(multivariate) and for individual traits (Burton et al., 2017; Poorter et al., 2019). Because SLA captures the effects of multiple physiological pathways, it is generally expected to be more plastic than leaf chemical traits (Lemke et al., 2015), although there is considerable variability in the plasticity of both morphological and chemical traits (Kuppler et al., 2020). In our study, SLA responded most strongly and positively to increased basal area (Figure 4). This is a typical response to reduced light availability, denoting a shift from water retention in high light, through thicker leaves with a lower surface-to-volume ratio and proportionally more mesophyll, to the maintenance of photosynthetic activity in low light through thinner leaves that favour more gas exchange (Poorter et al., 2019). The traits more specifically related to photosynthetic activity were also best predicted by canopy structure, but with smaller effect sizes than SLA. Thus, Leaf N, a

critical component of rubisco, and leaf cations K, Mg and Ca, which are involved in a suite of enzymatic pathways solicited by photosynthesis (Eichhorn et al., 2014), all showed weakly positive trends with increasing basal area. This is consistent with an overall decrease in photosynthetic activity on a per area basis, coupled with a stronger decrease in leaf mass per area (SLA^{-1}), leading to a small net-positive increase in mass-based nutrient concentration (Poorter et al., 2019).

In agreement with our prediction, climatic drivers also affected multivariate variability of aboveground traits, albeit with low effect size. Among individual traits, climate appeared primarily as a driver of Leaf P and (weakly) of Leaf Mg. Phosphorous acquisition can be modulated by water availability (Chen et al., 2013), and tends to increase consistently with temperature along altitudinal gradients (Midolo et al., 2019). Here, temperature ($\text{GDD}_{>5}$) had the largest

effect size, but in this case Leaf P was negatively associated with the number of growing degree days, which could be the result of covariates not considered in our study. Soil P accumulates during the weathering of parent material. Given the negative correlation between (latitudinal) temperature gradients and geological age, the effect detected in our study may thus be driven more by P availability in the soil than by temperature per se (Chen et al., 2013; Hou et al., 2018).

In contrast to our prediction, SLA was the only leaf trait affected by the neighbourhood competitive environment. These results support those of Burton et al. (2017), for whom understorey competitive environment was consistently selected as a predictor for leaf traits, but that explained only marginal amounts of variance. Although several studies found generalisable positive relationships between aboveground traits such as SLA, Leaf N, leaf size, height or stem density and the degree of competition (Bennett et al., 2016; Burton et al., 2017), finer-scale studies also suggest that aboveground ITV response to biotic factors may depend on overall species' strategy (Helsen et al., 2017), and involve complex compensation mechanisms in relation to belowground traits (Bennett et al., 2016).

4.1.2 | Root traits

If roots are organised to provide key functions to the plant such as nutrient and water acquisition (e.g. the 'Root Economics Spectrum'; Comas & Eissenstat, 2004; Roumet et al., 2016), one might expect traits related to nutrition and soil exploration to respond in a coordinated way to variation in soil fertility and drainage (Burton et al., 2017). Contrary to our prediction, multivariate root ITV was not strongly associated with environmental gradients, including soil conditions, and drivers of ITV only emerged for some of our univariate models. For instance, Root P was associated with site drainage, which may be related to site-level P availability under poor drainage conditions, but other traits were associated with canopy structure (Root N) and neighbourhood competitive characteristics (Root K, SRL). This contrasts with Burton et al. (2017), who found no effect of neighbourhood competition or light availability on SRL in similar forest systems. These results are, however, consistent with an overall response of roots to increased shade, whether from competing neighbours or from the canopy. In both these situations, plants can reallocate resources to leaves, promoting thinner and less dense root tissue, and increasing mass-based Root N (Bennett et al., 2016; Poorter et al., 2019; Weemstra et al., 2021).

We selected root traits to compare with leaf traits hypothesised to be part of the shared leaf and root economics spectrum (Reich, 2014). Although SRL and Root N are often used as analogues for SLA and Leaf N on the assumption that they capture belowground investment in resource capture (e.g. Roumet et al., 2016), these traits are only partially comparable. For instance, while Leaf N is almost entirely involved in photosynthesis (thus energy capture), Root N is involved in many more plant functions, including nutrient uptake, nutrient storage and plant defences, among others (Freschet

et al., 2021). Similarly, SRL does not fully capture the efficiency of resource uptake (Freschet et al., 2021; Weemstra et al., 2016). There is, therefore, reason to doubt whether these traits can capture simple trade-offs in resource uptake and investment. Recent studies investigating broader sets of traits point instead towards a root economic 'space', rather than 'spectrum' (Bergmann et al., 2020; Freschet et al., 2021; Weemstra et al., 2021). In this context, capturing the effect of environmental filters on multivariate ITV would require investigating traits that also reflect partnerships with symbionts, belowground resource allocation and root spatial distribution (e.g. mycorrhizal association and colonisation intensity, branching density, root hair length; Freschet et al., 2021). This high dimensionality of root traits can also lead to 'one-way benefits', whereby traits like SRL can experience strong selection for some trait values at the dry end of a water availability gradient, but many trait values can be equally successful under wet conditions (Laughlin et al., 2021). In sum, roots may find numerous ways to solve the same resource shortage (Freschet et al., 2021), and generalisable root trait-environment relationships may therefore be rare.

4.1.3 | Generalisable drivers of aboveground and belowground ITV

Overall, fixed effects in our univariate models explained an average of 7% aboveground and 2% belowground trait variability. Because random effects absorbed any remaining mean difference between localities and species (R^2_c , Figure 4), this leaves between 9% and 62% (roots) and between 16 and 48% (leaves) of variance unaccounted for. These high numbers beg for future comparison between our set of generalist species and co-occurring species that achieve broad geographical ranges through specialised strategies, like spring ephemerals (e.g. *Trillium* spp.) and shade specialists (e.g. *Oxalis montana*). One explanation for the unexplained variation in our study might be that we did not focus on the spatial scale at which ITV is most involved in environmental response among these generalists. We know that the drivers of ITV are scale-dependent (Messier et al., 2017). Therefore, while we focused solely on site-level values, it is possible that, for instance, within-site leaf ITV could be strongly structured by the environment and help individuals and populations respond to fine-scale heterogeneity in understorey light conditions.

Several mechanisms have also been proposed that might generate strong species-specific trait-environment relationships. For instance, if traits respond to the environment following a bell shape, both positive and negative slopes could occur for species sampled at different positions along the distribution (Albert et al., 2010). Indeed, Weemstra et al. (2021) found some evidence of a nonlinear response of SRL to MAP. Although we did not test for nonlinearity, this could be one explanation why we found no generalisable relationship between these variables. Alternatively, although we assumed strictly competitive neighbourhood effects, changes in the balance of competitive to facilitative relationships can also explain species-specific relationships along biotic gradients (Kichenin

et al., 2013). Furthermore, four of our study species have known associations with arbuscular mycorrhizae, while the fifth, *V. angustifolium*, is associated with ericoid mycorrhizae—generating another axis along which species-specific responses might emerge (Bergmann et al., 2020). Thus, there is good reason to expect idiosyncratic species trait–environment relationships above- and belowground (Albert et al., 2010; Burton et al., 2017; Helsen et al., 2017; Kichenin et al., 2013; Weemstra et al., 2021). One way to derive generalisable insight is to focus not only on the slope of trait–environment relationships, but also on the magnitude of environmental fit.

4.2 | Association between ITV and environmental fit

If species occupy niches along a given environmental gradient by changing their trait values to find the local optima (environmental matching, *sensu* Ackerly, 2003), then one might predict that species with more variable traits would occupy broader niches (Hermant et al., 2013; Mitchell et al., 2017; Sides et al., 2014; Treurnicht et al., 2020). Similarly, if we focus specifically on those species with especially broad ecological niches, we might predict that more variable traits would be associated with higher environmental fit, regardless of the direction of individual trait–environment relationships (Figure 1). Contrary to our hypothesis, we only found this association for a minority of traits, and primarily in response to climate.

Leaf traits respond plastically to shade (Poorter et al., 2019); hence, it is striking that higher between-site ITV in leaf traits was not associated with improved environmental fit with canopy structure. Typically long-lived, understorey species in mixed and boreal biomes can commonly go through contrasting phases—from effective colonisers after disturbance to long-term persistence under a closed canopy (Gilliam & Roberts, 2003). This range of behaviours may explain why probability of presence of such species has not been found to be correlated with aboveground traits (Thuiller et al., 2010).

In contrast, we found that belowground, increased Root K variability was associated with increased environmental fit with the competitive neighbourhood. Bennett et al. (2016) obtained similar results in controlled experiments where species with more variable root traits matched belowground competitive dynamics more closely. There is still much that we do not know about the physiological role of Root K, but there is some indication that it may be associated with abiotic and biotic stress tolerance (Wang et al., 2013). This warrants further research and raises the question of why we did not find this pattern along other potentially stressful gradients.

While we expected leaf traits would vary predictably according to climate (Midolo et al., 2019), we only found weak effects (Figure 3, Figure 4). Nevertheless, between-site ITV of SLA and Leaf N were associated here with increased environmental fit relative to climate. This complements the findings from Treurnicht et al. (2020) that ITV

of Leaf N is associated with greater niche breadth in temperature. Although these authors focused primarily on aboveground traits, we also found a positive relationship between ITV and environmental fit for SRL, despite only weak generalisable environmental drivers (Figure 4). This is an indication that, despite variability in the slope of root trait relationships with climate (Weemstra et al., 2021), ITV may be similarly involved in species' response to climate gradients above- and belowground.

While one advantage of focusing on environmental fit is that it is agnostic relative to slope sign, this comes at the cost of ignoring slope magnitude; thus, our approach only partially captures trait–environment relationships. Furthermore, because total trait variation is involved in the calculation of R_m^2 (our proxy for environmental fit), these two variables are mathematically related, and so it is not possible to draw conclusions about a causal link that might exist between them. Nonetheless, by looking at how ITV is partitioned for more or less variable traits (i.e. whether it is environmentally structured or unstructured), we can begin to look for general ways in which ITV might be involved in species' ability to adapt to broad environmental gradients. In our small group of widely distributed forest understorey species, traits with higher ITV were not associated with higher environmental fit across most of the environmental gradients that we investigated, with the exception of climate. Variability in these traits tended to remain unstructured. One explanation for the high level of unstructured variation among traits with high ITV is that ITV may be structured by other environmental drivers not included in our study, like seasonality. Another, not mutually exclusive explanation for this unstructured variation might be the existence of underlying genetic variation that is uncorrelated with environmental differences (Matesanz et al., 2010; Messier et al., 2017; Moran et al., 2016). Both structured and unstructured variation can play a key role in species' response to environmental gradients (Ackerly, 2003; Bolnick et al., 2011). Our results raise, but do not answer, the possibility that ITV might play different roles along different environmental gradients: further work will be needed to determine the implications of our results for species' adaptation.

The environmental matching hypothesis relies on two key predictions to explain species' niche breadth: first, between-site ITV responds to variations in the environment and, second, this should lead to improved fitness at the local scale (Ackerly, 2003). Both criteria must be met to exclude cases where (a) species derive an advantage from their average trait values, but with no direct involvement of ITV in meeting local optima, and (b) cases of purely plastic, but non-adaptive response. In our study, trait–environment relationships across species explained a modest proportion of between-site variability. When we looked at individual species' traits, however, we found some traits where more variability was associated with higher environmental fit, particularly in response to climate. To know whether these species achieve their considerable niche breadth via environmental matching, the next step will be to test whether the portion of ITV that was structured by the environment in our study resulted in higher fitness than would be expected from species' average trait values. Recent efforts to predict species' performance using

traits have yielded generally weak relationships (Paine et al., 2015). By refocusing efforts from interspecific to intraspecific relationships between trait, performance and the environment, there is tremendous potential to establish a closer link with evolutionary dynamics (Yang et al., 2018), and yield direct answers as to how ITV might be involved in explaining species' ecological niches.

Current forecasts for temperate and boreal forests predict increased temperature, reduced precipitation, and associated changes in disturbances and stand-level regeneration (Zhang et al., 2019). By asking how ITV contributes to the way species with broad ecological niches respond to underlying environmental gradients, we can begin to understand how different species might respond to projected changes. Even among a small set of species with similar ecological niches, our results suggest that, even if ITV of individual traits and individual species may be involved in environmental response, this is only weakly generalisable across species. At the species level, the association between ITV and environmental fit was not only rare, but also species specific. In our search for general ways in which species adapt to environmental variation and change, our results therefore remind us of the multitude of ways in which even a small set of understorey species with similar niches can overcome the same challenges.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

A.D.M., F.H., F.C., I.A. and N.T. conceived the methods; A.D.M., A.A., A.C.S.M., A.M., B.H., B.S., C.M., D.M., D.G., F.W.B., F.H., F.C., I.A., I.B., J.R.M., J.F.J., L.S., M.A., N.T., N.J.F., S.E.M., S.D. and Y.B.

collected the data; F.C., L.B.-M., B.B.K. and B.H. analysed the data; F.C., I.A. and A.D.M. led the writing of the manuscript. All authors provided critical comments on the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13894>.

DATA AVAILABILITY STATEMENT

Trait and environmental data for this study are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.jwstqjqbr> (Cardou et al., 2022).

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