













RESEARCH ARTICLE

Geographic scale and disturbance influence intraspecific trait variability in leaves and roots of North American understorey plants

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Abstract

1. Considering intraspecific trait variability (ITV) in ecological studies has improved our understanding of species persistence and coexistence. These advances are based on the growing number of leaf ITV studies over local gradients, but logistical constraints have prevented a solid examination of ITV in root traits or at scales reflecting species' geographic ranges.
2. We compared the magnitude of ITV in above- and below-ground plant organs across three spatial scales (biophysical region, locality and plot). We focused on six understorey species (four herbs and two shrubs) that occur both in disturbed and undisturbed habitats across boreal and temperate Canadian forests. We aimed to document ITV structure over broad ecological and geographical scales by asking: (a) What is the breadth of ITV across species range-scale? (b) What proportion

of ITV is captured at different spatial scales, particularly when local scale disturbances are considered? and (c) Is the variance structure consistent between analogous leaf and root traits, and between morphological and chemical traits?

3. Following standardized methods, we sampled 818 populations across 79 forest plots simultaneously, including disturbed and undisturbed stands, spanning four biophysical regions (~5,200 km). Traits measured included specific leaf area (SLA), specific root length (SRL) and leaf and root nutrient concentrations (N, P, K, Mg, Ca). We used variance decomposition techniques to characterize ITV structure across scales.
4. Our results show that an important proportion of ITV occurred at the local scale when sampling included contrasting environmental conditions resulting from local disturbance. A certain proportion of the variability in both leaf and root traits remained unaccounted for by the three sampling scales included in the design (36% on average), with the largest amount for SRL (54%). Substantial differences in magnitude of ITV were found among the six species, and between analogous traits, suggesting that trait distribution was influenced by species strategy and reflects the extent of understorey environment heterogeneity.
5. Even for species with broad geographical distributions, a large proportion of within-species trait variability can be captured by sampling locally across ecological gradients. This has practical implications for sampling design and trait selection for both local studies and continental-scale modelling.

KEYWORDS

functional biogeography, intraspecific trait variability, leaf trait, plant functional trait, root trait, specific leaf area, specific root length, tissue nutrient concentration

1 | INTRODUCTION

Interactions between genetic make-up and an individual's environment, expressed as trait variability, are at the core of today's most pressing questions in macroecology. More specifically, variability in plant traits can contribute much to our understanding of plant performance and fitness across environmental gradients (Keddy, 1992; Violle et al., 2012). Although less frequently characterized than between-species variability (Albert, Thuiller, Yoccoz, Soudant, et al., 2010; Le Bagousse-Pinguet, Bello, Vandewalle, Leps, & Sykes, 2014; Garnier, Navas, & Grigulis, 2015), intraspecific trait variability (ITV), that is, trait variability among individuals of a single species, is increasingly being recognized as a major factor for species coexistence and persistence in a changing environment (Butler et al., 2017; Shipley et al., 2016; Violle et al., 2012). By formally taking ITV into account, community ecologists have improved both detection of community assembly mechanisms (Le Bagousse-Pinguet et al., 2014; Jung, Violle, Mondy, Hoffmann, & Muller, 2010; Siefert, 2012) and prediction of global change impacts on ecosystem processes (Jackson, Peltzer, & Wardle, 2013; Wardle, Bardgett, Walker, & Bonner, 2009).

There is now good evidence that the general assumption that ITV is lower than interspecific variability does not hold true in all situations (Kazakou et al., 2014; Kichenin, Wardle, Peltzer, Morse, & Freschet, 2013; Kumordzi, Nilsson, Gundale, & Wardle, 2014). The crucial question that emerges is, therefore, when and why is ITV more important? Previous studies have suggested that ITV is a mechanism by which plant species respond to local spatial resource heterogeneity (Valladares, Gianoli, & Gómez, 2007) and is related to environmental variation across the species' range (Helsen et al., 2017). Intraspecific trait variability may be particularly important in low diversity ecosystems where reduced competition could allow individuals of the same species to occupy a larger trait space (Freschet, Bellingham, Lyver, Bonner, & Wardle, 2013; Silvertown & Charlesworth, 2009; Violle et al., 2012). For species with widespread geographical distributions (Fajardo & Piper, 2011; Sides et al., 2014), greater ITV could represent better adaptation to a wide range of environmental conditions (Albert, Grassein, Schurr, Vieilledent, & Violle, 2011; Sides et al., 2014; Vasseur et al., 2018). The *spatial variance partitioning hypothesis* predicts that ITV will saturate with increasing spatial scale (Albert et al., 2011) and therefore a large proportion of the variability should be observed at the local scale (Burton et al., 2017).

Environmental variations can create strong selective forces and impact trait variability both within and among plant organs (Freschet, Swart, & Cornelissen, 2015; Reich et al., 1999). In North American boreal and temperate forests, natural and anthropogenic disturbances such as fire, pest outbreaks, wind-throw and logging are common disturbances that can drastically alter the availability and distribution of above- and below-ground resources (Venier et al., 2014). This disturbance-driven, small-scale heterogeneity is nested within continental-wide climatic gradients of precipitation and temperature. Spanning over 5,200 km longitudinally, mean annual precipitation in Canada can be as low as 300 mm in the West-Central Boreal Forest and up to 1,800 mm in some regions of Eastern Canada (Canadian National Vegetation Classification, 2015). Some understorey plant species have remarkable adaptation to these multi-scale environmental variations, such that they display both a vast geographical (spatial) extent (Table S2; Figure S1 in Supporting Information) and a broad ecological range (i.e. suitable environmental gradient). ITV could explain their wide extent but it may also contribute to the maintenance of fitness in fluctuating understorey environmental conditions at local scales (Aubin, Messier, & Kneeshaw, 2005; Bartemucci, Messier, & Canham, 2006; Neufeld & Young, 2003).

Despite the ecological importance of disturbance in these forests (Bonan & Shugart, 1989; Venier et al., 2014), relatively little is known about how disturbances influence the magnitude of leaf and root ITV. Standard trait measurement protocols were developed to address ecological questions involving interspecific comparisons; since these protocols recommend selecting mature plants in full light and without physical damage (e.g. Pérez-Harguindeguy et al., 2013), intraspecific variation is likely underestimated. This is particularly the case for forest plants that thrive in both the understorey and open, post-disturbance stands. Considered as common within their distributions, these understorey herbs and shrubs have garnered less attention than rare, economically valuable or invasive species. Spanning both wide spatial (distance) and ecological gradients, these species are expected to have a high magnitude of ITV (Sides et al., 2014). Their ubiquity makes them particularly suited to address questions about the ecological importance of ITV for species persistence.

An important question is whether ITV varies among plant organs. Theory suggests that plants allocate internal resources differentially among organs to maximize capture of the most limiting resource (e.g. Freschet et al., 2013). For instance, in low-light conditions, plants should allocate significantly more resources to leaves than to roots. Because plant response to environmental stimuli is determined at the whole-plant level (Freschet et al., 2015; Kang, Chang, Yan, & Wang, 2014), several authors have suggested that trait co-variation should be constant across spatial scales (Liu et al., 2010; Reich et al., 1999). If this holds true, variation in leaf traits could be used as proxies for the harder to measure analogous root traits. However, recent evidence from empirical studies shows that trait variability can be decoupled among organs and across species (Freschet et al., 2013; Kumordzi, Gundale, Nilsson, & Wardle, 2016), with different

patterns emerging at different ecological (Messier, McGill, Enquist, & Lechowicz, 2016) or spatial scales (Kang et al., 2014). For example, Liu et al. (2010) demonstrated greater variability in leaf traits than in analogous root traits at broad spatial scales. In these cold, nutrient-limited boreal soils, we might expect greater variability of SRL and root nutrients at the largest scale, since changes in soil mineralogy, and hence pH and nutrient availability, may be most important at this scale (Boiffin, Aubin, & Munson, 2015). Within plant organs (e.g. leaves), nutrient concentrations were found to exhibit higher ITV than morphological traits (Kazakou et al., 2014).

In theory, ITV should be estimated by systematic sampling of individuals across a species' geographic and/or ecological range (Albert et al., 2011; Albert, Thuiller, Yoccoz, Soudant, et al., 2010). However, this is both impractical and unrealistic in most cases (Baraloto et al., 2010). Studies interested in ITV have therefore mainly focused on intensive local-scale sampling, measuring several individuals growing in contrasting environmental conditions (e.g. Albert, Thuiller, Yoccoz, Douzet, et al., 2010; Messier et al., 2016). Faced with logistical constraints, large-scale studies have relied primarily on meta-analyses, focusing instead on the relative contribution of leaf ITV to within- and among-community trait variance (e.g. Siefert et al., 2015). Gap filling approaches have typically been used to overcome partial coverage (Butler et al., 2017). Despite the notable progress that has been made in quantifying ITV, few studies have tackled range-scale estimates of ITV. This latter knowledge is necessary for a robust application of a trait-based approach to answer continental- and global-scale questions regarding climate change adaptation (Aubin et al., 2016; Violle, Reich, Pacala, Enquist, & Kattge, 2014). It is also important for local-scale studies, since without range-wide ITV estimates, trait values estimated from local measurements or data banks remain without context. Finally, knowledge of ITV at different spatial and ecological scales could provide guidance on the scale at which the majority of ITV is captured, reflecting the potential effect of ITV on ecosystem function.

In the present study, we investigate the magnitude of intraspecific variability in leaf and root traits across different spatial and ecological scales, for six ubiquitous understorey herb and shrub species that occur both in disturbed and undisturbed habitats across boreal and temperate Canadian forests. The two shrubs can be considered more conservative species, while the four herbs less conservative, but all are adapted to less fertile soils (Larsen, 1980). To achieve this sizeable sampling goal, we adopted a collaborative approach, collating the efforts of 23 field teams across Canada (Co-VITAS project). Strategically focusing on traits that could reliably be sampled by several field teams independently, we also chose traits related to the leaf and (potentially) root economics spectrum (Weemstra et al., 2016; Wright et al., 2004). The traits selected are among the most plastic (Siefert et al., 2015) and should respond to disturbance (SLA to light after canopy disturbance, and SRL to changes in nutrients associated with abiotic gradients of soil fertility that change over large scales, but also with disturbance; Boiffin et al., 2015). Plant nutrition (leaf and root N, P and cation bases) in acidic boreal soils is highly related to soil pH,

which also varies with large-scale changes in soil mineralogy and with soil disturbance, especially fire (Thiffault, Bélanger, Paré, & Munson, 2007).

This study was designed to document ITV structure over wide geographical (spatial) and ecological scales by sampling species throughout their range and under different disturbance conditions. More specifically, we address the following questions: (a) What is the breadth of ITV across species ranges, and how does it differ among species? We would expect the breadth to vary with species strategy and functional type (higher ITV across species ranges for herbs due to constraints on more conservative woody plants, Maire et al., 2013); (b) What proportion of ITV can be captured locally? A higher proportion of ITV should be found at smaller scales (Albert et al., 2011). Disturbance that removes the canopy should increase this proportion at smaller scales, since understorey species are particularly sensitive to altered light and soil conditions. The inclusion of a disturbance gradient adds ecological distance between samples to capture a larger proportion of ITV within a short spatial gradient; and (c) Is the variance structure across scales consistent between morphological and chemical traits, and between analogous leaf and root traits? Based on previous studies, we would expect higher ITV for chemical compared to morphological traits (Siefert et al., 2015). Leaves and roots may show similar variance structures among scales, but their response to disturbance-related changes in light and soil resources could cause differences in the proportion of variance explained at the local scale. Since light availability varies considerably between disturbed and undisturbed plots, we would expect higher variation for leaf than root traits at the plot scale. For root traits, we expect a higher proportion of the variance explained at a larger scale, related to changes in soil mineralogy.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted by 23 teams as part of the Co-VITAS project (Table S1) following a standardized protocol to characterize 79 plots across the boreal and temperate forests of Canada (Figure 1). Chosen locations were most often pre-existing study sites for which collaborators had ready access and knowledge (Table S1). Locations were selected to reflect the predominant continental climatic gradient across Canada and to capture a large extent of each species' range (Figure S1).

The Canadian continental gradient is characterized by an east–west decrease in mean summer rainfall. Of our study locations, the highest average summer rainfall (July–August) values occur in Quebec (Forêt Montmorency, 144 mm, 1971–2000, McKenney et al., 2011) and the lowest in northern Alberta and the Yukon (both 63 mm; 1971–2000; McKenney et al., 2011). Predictably, mean summer temperature across Canada tends to decrease with latitude and the lowest mean summer temperature (mean of July–August) of 13.4°C was recorded at the Yukon location (Kluane; McKenney et al., 2011) and the highest mean summer temperature of 24.4°C at Mont Saint-Hilaire, Quebec.

2.2 | Sampling design and data collection

Plant populations were sampled between 10 and 25 July 2014, following a nested hierarchical design (Figure 1). Our 79 study plots, reflecting both disturbed and undisturbed conditions, were nested within 32 localities distributed across four biophysical regions and spanning 5,200 km (Figure 1). We defined the sampling hierarchy as follows (from smallest to largest):

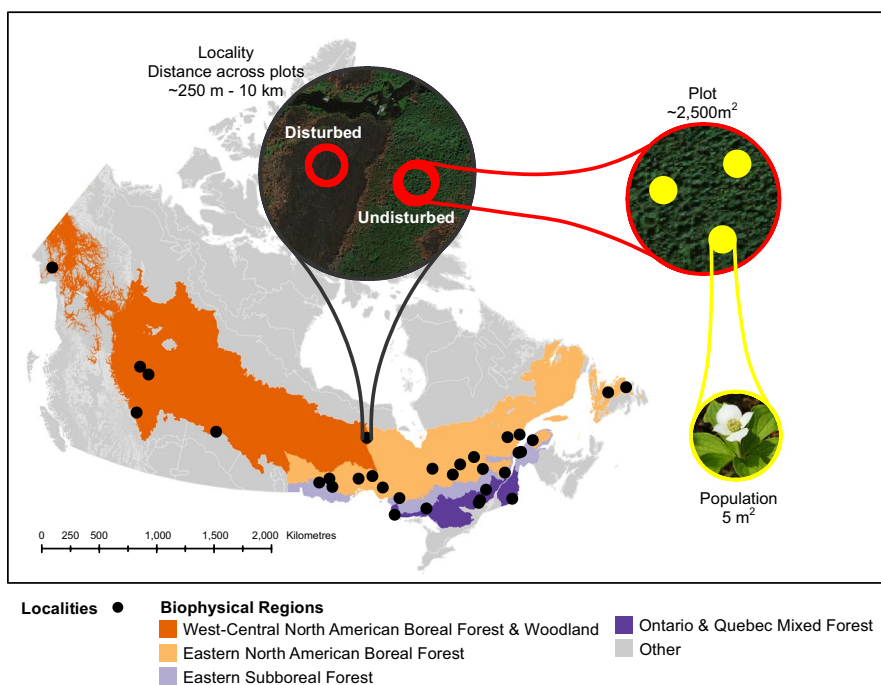


FIGURE 1 Spatial-scale hierarchy and nomenclature used in the study. Overall, 818 populations (5 m²) were sampled across 79 plots (2,500 m²) with and without disturbance, which were nested within 32 localities in four biophysical regions of Canada. Scale: Populations were located 50 to 100 m apart and were pooled at the plot level for analysis. Distance between disturbed and undisturbed plots was between 250 m and 10 km. The shortest distance between localities in the same biophysical region was 26 km. Localities were distributed across four biophysical regions and spanning 5,200 km. Map adapted from the Canadian National Vegetation Classification (Canadian National Vegetation Classification, 2015)

- (i) *Plot*: An area of approximately 2,500 m² where populations of the target species were sampled. The plot is located in one of the two following categories reflecting the local disturbance regime: “Undisturbed” mature closed canopy forest, with no sign of recent disturbance; or in a recently (less than 20 years) “Disturbed” forest affected by canopy removal and varying soil disruption (fire, wind-throw, insect outbreak, tree harvest, smelter deposition).
- (ii) *Locality*: A geographic location characterized by homogeneous climate regime and soil conditions, encompassing disturbed and undisturbed plots. These typically reflected each field team's study area. Localities included at least one plot and up to four, which were separated by distances of up to 10 km.
- (iii) *Biophysical region*: A regionally distinct vegetation zone reflecting differences in climate regime, soil conditions and forest composition, abundance and/or dominance. This refers to the “macro-group” level of the Canadian National Vegetation Classification System (Canadian National Vegetation Classification, 2015; <http://cnvc-cnvc.ca>). Biophysical regions included 3 to 16 localities each.

Selected sites had generally flat terrain, with slopes not exceeding 5%, and contained as many target species as possible. The resulting sampling design is summarized in Table S1.

2.3 | Target species and functional trait measurements

We focused on six common understorey plant species that occur in temperate and boreal forests of North America (Tables S1 and S2; Figure S1). These included two low shrubs: *Vaccinium angustifolium* (Ericaceae) and *Kalmia angustifolia* (Ericaceae), and four herbs: *Maianthemum canadense* (Asparagaceae), *Cornus canadensis* (Cornaceae), *Trientalis borealis* (*Lysimachia borealis*, Primulaceae) and *Aralia nudicaulis* (Araliaceae). The shrubs could be considered to have a more conservative strategy (slow-growing), in contrast to the herbaceous species. In particular, *Aralia* is found in higher fertility environments compared to the other three herbs.

For each target species present in a plot, three populations (i.e. ramets and/or individual plants located within a homogeneous ~5-m² area) were selected approximately 50 m apart. For each population, we pooled collected leaf material from 3 to 5 individuals. Fully expanded current-year leaves were collected in sufficient quantity to produce 2 g of dry weight material (10–30 leaves, ground through a 20-mesh screen using a Wiley mill). Leaf area of fresh material was captured by individual field teams before drying using scanners or cameras. All leaf samples were shipped to Great Lakes Forestry Centre (Sault Ste-Marie) for grinding. Nutrient analyses were carried out at Université Laval (Québec) and at Ministère des Forêts, de la Faune et des Parcs (Québec).

Similarly, for each population, the entire root system was gently extracted for 3–5 mature individuals making sure to include at least 10 absorbing fine roots. The samples were stored fresh in sealed

plastic bags with a moist paper towel for processing in the laboratory. Fresh roots were shipped in insulated containers to central laboratories for rapid, standardized processing: *Cornus* and *Maianthemum* roots to Université du Québec en Abitibi-Témiscamingue (Rouyn-Noranda) and the other species to Université Laval (Québec City).

A total of 818 target species populations were sampled (Tables S4 and S5). For each population, we estimated the specific leaf area (SLA) as the ratio of the leaf area to dry weight (cm²/g) and specific root length (SRL) as the ratio of root length to dry mass of fine roots (m/g). We measured SRL on absorptive fine roots, that is the most distal fine roots with healthy terminal root cap (Cornelissen et al., 2003). Ground leaf samples were pooled by population while ground root tissue had to be pooled at the plot level due to the small size of fine rooted species. Subsamples for each leaf and root sample were digested in H₂O₂Se (Lowther, 1980) to determine the concentrations of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). Following digestion, concentration of N in the digest was measured by spectrophotometry (FIAstar Tecator), P, by inductively coupled plasma analyses, and cations through atomic absorption (Optima 4300DV of Perkin-Elmer). The leaf and root morphological trait data were averaged within plot for consistency with nutrient root traits (i.e. one value per plot for each species/trait).

2.4 | Statistical analyses

All statistical analyses were performed in R (version 3.1.1., R Development Core Team, 2014) on data averaged per plot. First, to examine the breadth of ITV across each species' sampled range (question 1), we computed density plots showing the relative frequency of morphological (SLA and SRL) and chemical ([N], [P], [K], [Ca], [Mg]) leaf and root trait values for each of the six species ('ggplot2' package, Wickham, 2009). For each species and trait, we computed ITV as the coefficient of variation (CV_{trait}), which is estimated as the standard deviation of each distribution divided by the mean, in order to quantify the extent of trait variability across the entire species' distribution sampled. This provides a visual comparison of the trait variability for different species and traits. We were also interested in assessing the percentage of range-wide ITV that can be captured locally when sampling across the disturbance gradient (question 2). For each species and trait, the average and the maximum ITV observed between plots from a same locality were divided by the ITV measured across the species' sampled range.

We explored how the variance structure differs between leaf and root traits, and between morphological and chemical traits (question 3). This was done for each species individually because of the strong interactive effect of species and trait on ITV (results not shown). For each species and trait, the variance structure across sampling scales was determined using a mixed modelling technique ('lme4' package, Bates et al., 2015). Using trait values as response variables, our model included all three sampling scales as nested random variables: biophysical region (i.e. comparison among region), locality (i.e. comparison among localities) and plot (i.e. comparison between disturbed and undisturbed plots). For each trait, we then

decomposed and quantified the variance across sampling scales and expressed it as a percentage of the total variance explained by random components, yielding the variance structure across scales.

These analyses were conducted with consideration for the unbalanced nature of our study design (Gelman & Hill, 2007). We acknowledge that variance estimates for sampling scales with lower replication are less accurate than those for scales with higher replication.

3 | RESULTS

The studied species had quite different trait distributions, as demonstrated by their density plots (Figure 2), with clear differences among species in the mean, the mode and the breadth of their trait distribution. Some species, such as *V. angustifolium*, tended to have narrow trait distributions, while others displayed a generally wide breadth of trait values (e.g. *T. borealis*). The relative position of the mean trait values among species (x-axis, Figure 2) was consistent across traits. For example, the shrubs *Kalmia angustifolia* and *V. angustifolium* generally exhibited lower mean trait values and trait breadth than the herbs *A. nudicaulis* and *T. borealis* (Figure 2). In general, the two shrubs showed lower mean and breadth for leaf and root tissue

bases (Ca, K, Mg), compared to the herbs. Distributions are generally relatively flat for tissue K, and for leaf P and Mg, for herbaceous species. This pattern is much less evident for N, where the distribution is relatively constant across species (except *Aralia* characterized by higher mean N). Density plots showed that trait distribution breadth within species was largely consistent for both leaf and root traits, although root traits tended to vary less than leaf traits (Figure 2).

We observed differences in the coefficient of variation for analogous traits (similar traits measured on leaves and roots; Figure 3). For all species, the CV of SRL was greater than the CV for SLA; but for *C. canadensis*, they were similar. For most species, N and P were characterized by higher variability in roots compared to leaves; this was not the case for base cations, Ca, Mg and K, which showed no general pattern among species. The CV of leaf N was consistently lower for all species when compared to other traits (Figure 3).

It was possible to capture a substantial proportion of the trait variation locally when sampling both disturbed and undisturbed plots. Maximum range-wide ITV captured locally varied from 32% to 100% (61% on average for all traits and species; Table S3). On average, 22% of the range-wide ITV was observed between plots of a given locality. A larger proportion of leaf trait variation tended to be captured locally in comparison with roots (ANOVA, $p = 0.052$).

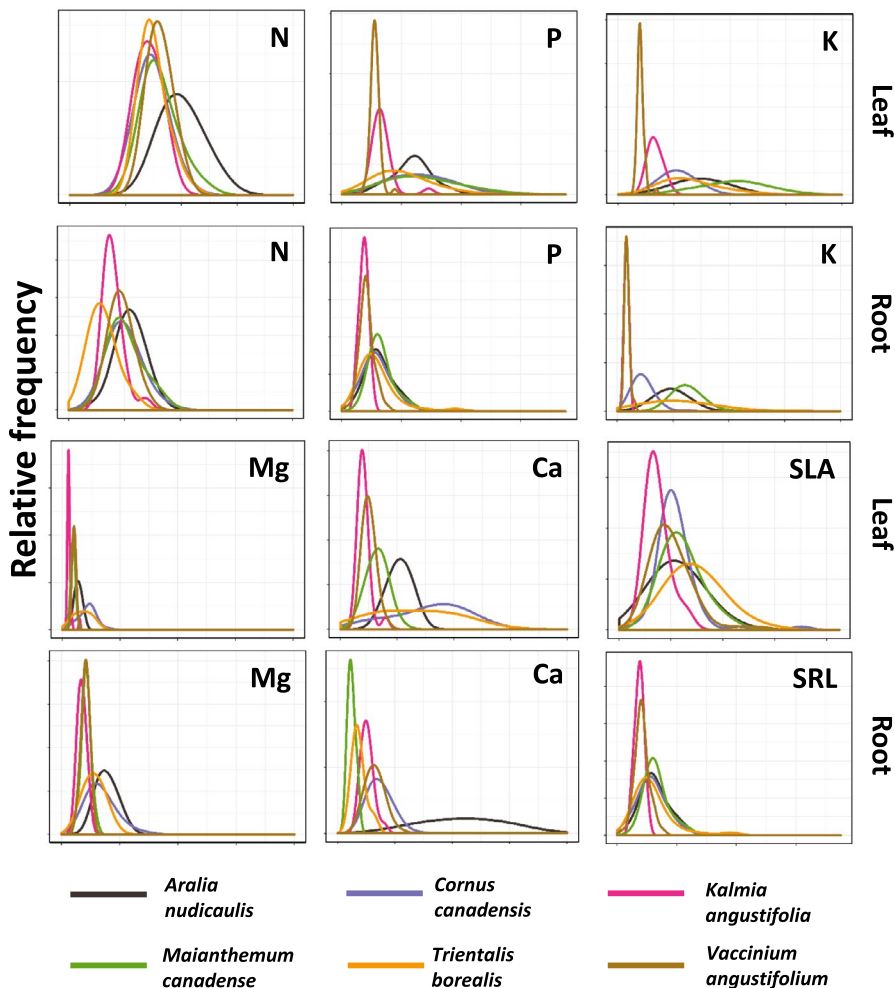
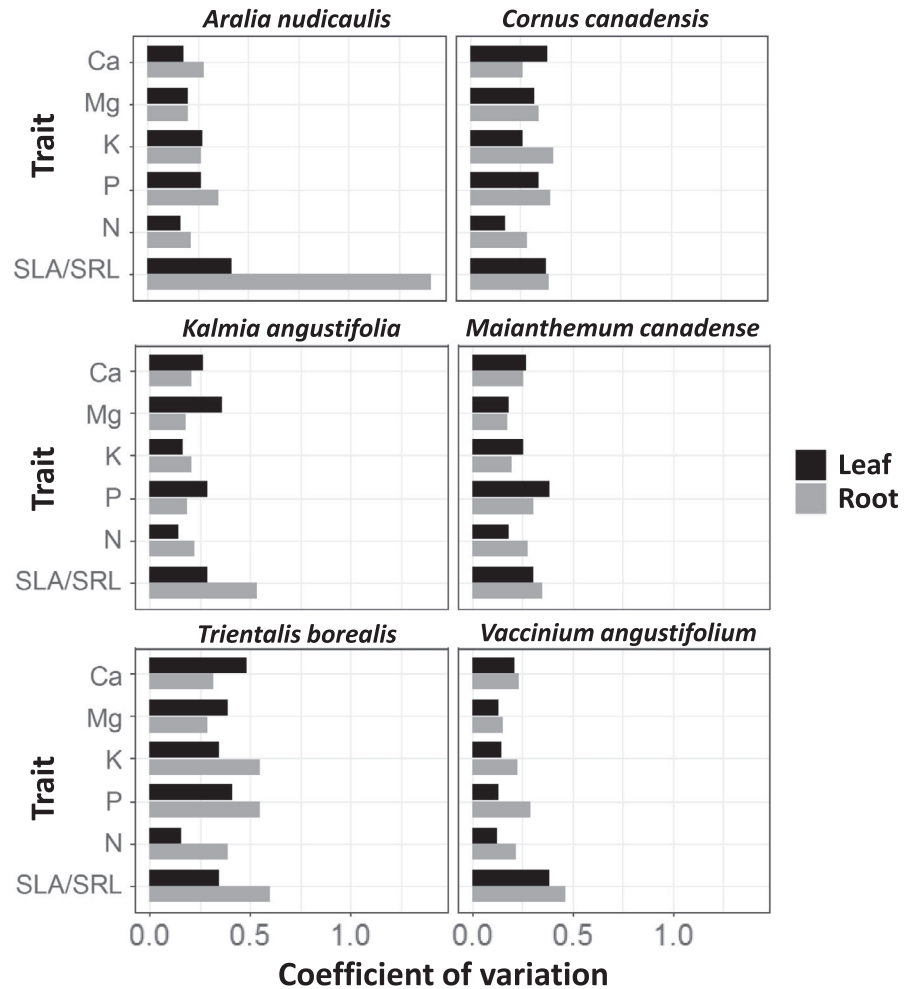


FIGURE 2 Relative frequency of measured root and leaf traits of six study species distributed across Canadian boreal and temperate forests. SLA, specific leaf area; SRL, specific root length; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium concentrations

FIGURE 3 Coefficient of variation of analogous morphological and chemical traits for each of the six study species, estimated for samples from across the geographical range of the species. SLA, specific leaf area; SRL, specific root length; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium concentrations



The variance structure revealed differences in the proportion of variance explained by the different sampling scales among species and across traits (Figure 4). Figure 5 shows the average cumulative proportion of trait variance explained at each scale. We observed a clear decrease in the proportion of explained ITV with increasing spatial scale (Figure 5), which confirms that overall a substantial amount of ITV can be captured at the plot scale when sampling both disturbed and undisturbed plots within a locality.

The proportion of ITV captured at each scale differed for root and leaf traits (Figures 4 and 5). For leaf traits, differences among plots captured on average, 10 to 49% of the total ITV (Figure 5), while extending sampling to include multiple localities added an additional 18 to 54% to the total proportion of ITV explained for an average species. Large-scale sampling among biophysical regions captured an additional 3 to 18% of leaf trait variability. For chemical root traits, with the exception of Ca, sampling at the plot level explained 23 to 45% of the total proportion of chemical root trait variance, while extending sampling among localities added an additional 19 to 30%. Sampling these chemical root traits at a large scale explained an additional 3 to 10% of variance. For Ca, only 4% of variance occurred at the plot level, while sampling among multiple localities added an additional 45%. Sampling among biophysical regions added another 3% variance captured (Figure 5).

For SRL, 13% of variance occurred at the plot level, an additional 28% was captured among multiple localities, and sampling among regions only added an additional 3%. The relatively low amount of ITV explained at the biophysical region scale (among regions) was generally consistent for most species with some exceptions, such as *V. angustifolium* root P, and leaf Ca, and *A. nudicaulis* leaf traits (Figure 4).

We found strong contrasts in the relative contribution of sampling scale for analogous above- and below-ground traits. For instance, leaf Ca and SLA had the lowest proportion of variance not accounted for by our model (on average 18 and 24%, respectively) and SRL the highest (54%; Figure 5). Similarly, 85% of SLA variance for *V. angustifolium* occurred among plots, while SRL variance for this species was very low at that scale (4%; Figure 4).

4 | DISCUSSION

4.1 | Magnitude of ITV for different species

The magnitude of ITV is expected to reflect the extent of environmental heterogeneity (Valladares et al., 2007) and should indicate the relative contribution of environmental drivers to phenotypic variation (Messier et al., 2016). We report range-scale estimates

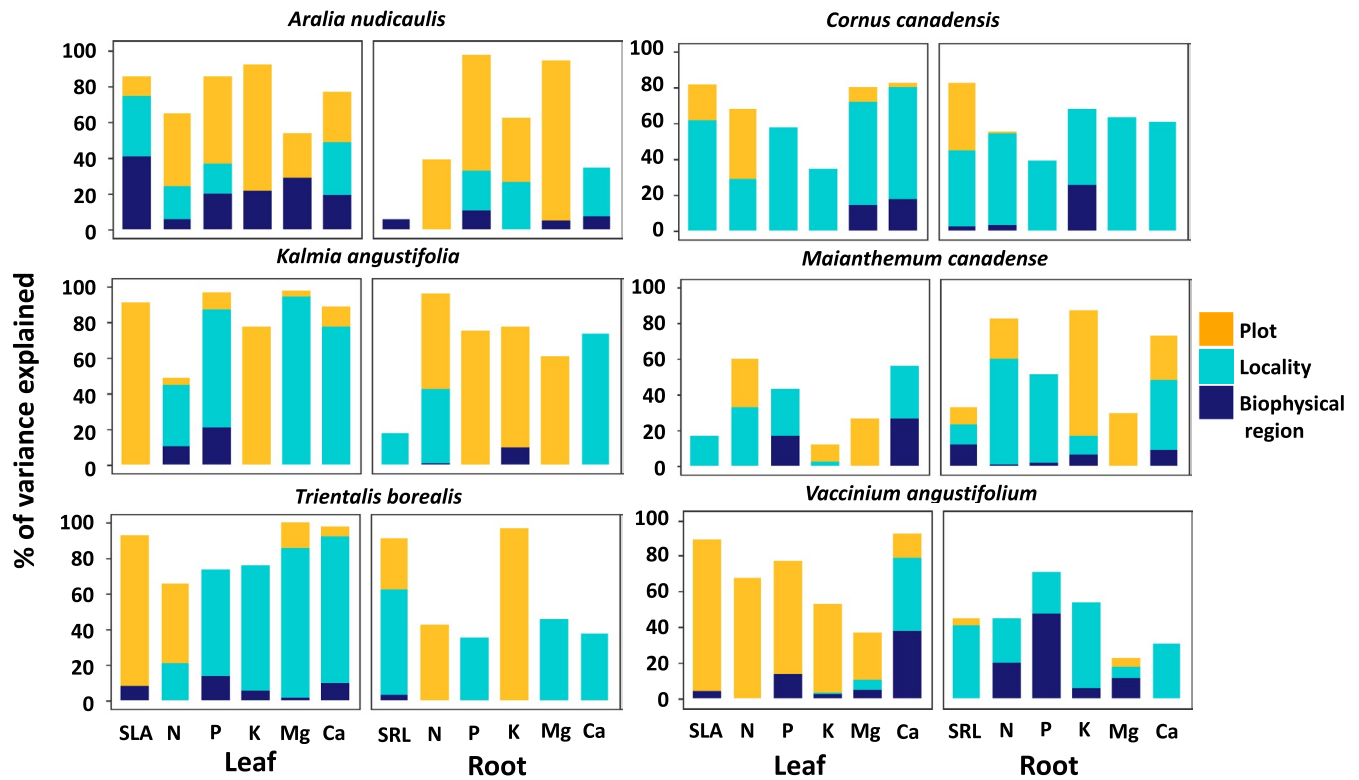


FIGURE 4 Summary of variance decomposition analyses showing the relative contribution of the three sampling scales to variability in morphological and chemical traits measured on leaf and root tissues for six study species. SLA, specific leaf area; SRL, specific root length; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium concentrations

of root and leaf ITV for six North American understorey species with wide geographical and ecological distributions (Figure 2). Such range-scale estimates are extremely rare, especially for root traits, and it is the first time that ITV estimates are reported for North American understorey ubiquitous species. Different trait distributions are evident among the six species, highlighting important differences in magnitude of ITV (Figure 2). The most consistent pattern (and lower CV; Figure 3) among species was noted for leaf N, and to a lesser extent, SLA; this could be related to the leaf economics spectrum. *A. nudicaulis*, the most nutrient-demanding species (associated with fertile sites), demonstrates a wider curve for leaf N and SLA, and a higher mean leaf N. The two shrub species show generally narrower breadth and lower means for most traits, especially tissue base cations, perhaps related to their preference for low fertility environments (Thiffault, Titus, & Munson, 2004). Strategies, then, do have some impact on trait probability distributions. In general, SRL has a higher CV than other traits (Figure 3); this may reflect the heterogeneous character of soils, in terms of mineralogy, texture and drainage (Weemstra et al., 2016).

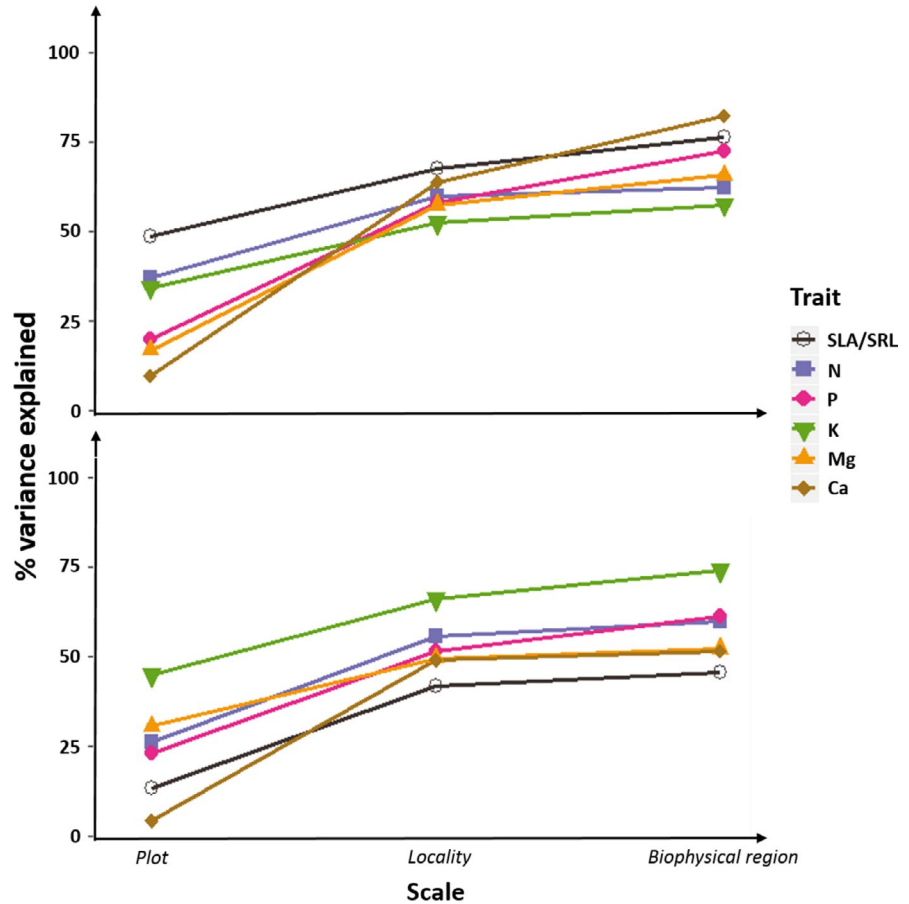
4.2 | Partitioning of ITV at three scales

For most traits, we found a low proportion of ITV captured at large spatial scales (i.e. among biophysical regions; Figure 4). We observed that the greatest proportion of ITV occurred locally among populations from contrasting environments (i.e. in disturbed and

undisturbed plots) and among localities from a given biophysical region. These results are in accordance with the spatial variance partitioning hypothesis (Albert et al., 2011), which predicts that ITV should saturate with increasing scale, as well as with studies that noted a high proportion of variance explained locally (e.g. Moreira, Tavsanoğlu, & Pausas, 2012; Lajoie & Vellend, 2015; Messier et al., 2016). North American boreal and temperate forest understoreys are the result of environmental gradients operating at different scales, including continental climatic gradients and local heterogeneity driven by anthropogenic and natural disturbance regimes (Bonan & Shugart, 1989; Schulte & Mladenoff, 2005). In particular, canopy removal after a disturbance such as fire or harvesting causes major shifts in understorey environmental conditions, notably light availability, temperature and soil moisture regime (Neufeld & Young, 2003; Ross, Flanagan, & Roi, 1986; Venier et al., 2014). The important contribution of disturbance to the ITV of these six ubiquitous species underlines their adaptation to disturbance-prone environments.

Although there were clear differences in ITV response across spatial scales, no general trend emerged among species. Each species demonstrated quite different partitioning with no similarities among species according to strategy, nor differences between herbs and shrubs, this latter observation supporting the results of the meta-analyses by Siefert et al. (2015). The greatest proportion of trait variance explained for the two most common herb species, *T. borealis* and *C. canadensis*, tended to be captured in nutrients at the locality scale, indicating a broad adaptability to heterogeneous

FIGURE 5 Average magnitude of intraspecific trait variability in leaf (top panel) and root traits (bottom panel) for the six study species observed across different sampling scales. SLA, specific leaf area; SRL, specific root length; N, nitrogen; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium concentrations



soil nutrient conditions (Figure 4). A high proportion of SLA variance was also captured at the locality scale for *C. canadensis*. This would seem to indicate a wide above-ground plasticity and adaptation to different light conditions created by disturbance. The lowest variance at the locality scale was noted for leaf traits of *V. angustifolium*, a conservative species. For this species, a large proportion of leaf trait variance was captured at the plot scale (i.e. between disturbed and undisturbed plots).

Among leaf traits, SLA, which is known to vary strongly with light and temperature and moderately with nutrient availability (Poorter, Niinemets, Poorter, Wright, & Villar, 2009), showed the highest proportion of explained variance at the plot scale (Figure 5). Most of the variation in SLA was captured among plots reflecting differences in light availability, and much less variation was accounted for by sampling from several localities or from different biophysical regions. In contrast, a very low proportion of leaf and root Ca was captured among plots but a substantial proportion was captured when sampling among localities, perhaps related to soil mineralogy.

While our results indicate ITV saturation with increasing spatial scale as predicted by Albert et al. (2011), they also highlight the importance of adequately covering the entire species niche in ITV assessments. Our results clearly show the importance of sampling across contrasting environmental conditions in order to capture the full extent and magnitude of ITV for species with a broad ecological range. We build on the model prediction of Albert et al. (2011) by

accounting for species' range sizes and propose that ITV can increase with spatial scale until the full breadth of a species' ecological niche is covered (including the full range of environmental conditions in which it can maintain non-null fitness). ITV can then be expected to taper off at the geographical scale where genetic variation becomes the main driver of phenotypic variability (Vasseur et al., 2018). It is important to note that our study design does not allow us to discriminate between purely spatial scale (i.e. the physical distance between samples) and ecological scale (i.e. the distance between samples in terms of the underlying environmental gradient) at the local level. The drivers of disturbance-related ITV and continental-scale ITV may be different and independent of each other.

A large proportion of the variability in leaf traits remained unaccounted for by the three sampling scales included in the design (31% on average, Figure 5). In a study investigating ITV structure from plot level down to the leaf level, Messier et al. (2016) accounted for 49% of the SLA variance and 33% of the leaf N variance at ecological scales lower than our sampling design (individual, sampling strata and leaf scales). This was attributed to variations in leaf vertical position, understorey light heterogeneity and individual phenotype (Messier et al., 2016). Residual variance in our study, therefore, could potentially be attributable to leaves, individuals and populations sampled. The proportion of variability in root traits unaccounted for by our three sampling scales was similar to that for leaf traits (40% on average, Figure 5), with the exception of SRL for which the proportion

was higher (54%). The high variance unaccounted for by our study design underscores the necessity of sampling traits at smaller ecological scales (e.g. individuals and leaves or roots).

Several studies have emphasized the need to adequately capture ITV to better understand its contribution to large-scale ecological processes (Le Bagousse-Pinguet et al., 2015; Siefert, 2012; Violle et al., 2012). Obviously, documenting ITV for species with extended geographical distributions involves a major logistical commitment. However, our findings suggest that a large proportion of ITV (averaging 22% of the range-wide ITV; Table S3) is driven by ecological gradients that are found over short distances (disturbed vs. undisturbed), while a smaller part of ITV is the result of environmental gradients spanning over large geographical extents (e.g. climate and soil type). Therefore, local measures of ITV may be adequate estimates of species' ITV when broad ecological gradients are locally available. However, depending on study objectives, quantifying the greatest proportion of ITV may be insufficient (Albert et al., 2011). For instance, even small amounts of ITV captured at large scales may be important for biome-scale sensitivity analyses or climate change adaptation studies (Anderegg, 2015; Aubin et al., 2018).

4.3 | Correspondence between above- and below-ground ITV

In answer to the third question, we addressed whether the variance structure across spatial scales was consistent between analogous leaf and root traits, and between morphological and chemical traits. Chemical traits showed lower variation than morphological traits (Figure 3). However, SLA and SRL are considered to be among the most plastic morphological traits (Auger & Shipley, 2013; Siefert et al., 2015). Siefert et al. (2015) also found SLA more variable than leaf nutrients. Covariance in leaf and root traits has been observed across species in several studies (Reich et al., 1999, 2003; Westoby, Falster, Moles, Vesk, & Wright, 2002); however, we did not observe this covariance in our six understorey species. The leaf economic spectrum (Wright et al., 2004) was well expressed in our dataset, with more acquisitive species (*T. borealis* and *Maianthemum canadense*) having a higher SLA and leaf N concentration than the more conservative species (*Kalmia angustifolia* and *V. angustifolium*, Figure 2). However, we did not find any indication of an analogous coordination in the roots (i.e. a root economic spectrum; Roumet et al., 2016; Weemstra et al., 2016).

Our results suggest that the magnitude of ITV present in plant traits depends on the specific plant organ. Distinct organ-level ITV may not be surprising, as leaves and roots play different roles in plant resource acquisition and conservation strategies, and may consequently respond differently to drivers of phenotypic variability (Freschet et al., 2013; Kumordzi et al., 2014; Messier et al., 2016). More importantly, they are also exposed to vastly different environments, where local-scale disturbances have different implications. Disturbances resulting in canopy removal modify soil conditions, including increased soil temperature, microbial activity and nutrient availability (Venier et al., 2014); such changes could drive the root

trait variability observed among plots. Some of the unaccounted variance in root traits may also be attributable to the inherent difficulty of measuring roots; the imprecision in SRL measurement for the finely rooted species (e.g. *Kalmia angustifolia* and *V. angustifolium*) may, in part, explain their large CV (Figure 3) and high proportion of variability unaccounted for by the three sampling scales (Figure 4). However, *Maianthemum canadense*, a species with much thicker fine roots, also had a low explained SRL variance (Figure 4), suggesting an important role for processes occurring at smaller scales (e.g. nutrient availability) that differentially affect the individuals (supported by unpublished data, Munson and Corrales).

Chemical traits were more consistently structured across spatial scales (Figure 5), indicating a covariance among chemical root and leaf traits *on average*, despite variability among species (Figure 4; Figure S2). In comparison with leaf traits, ITV in roots remains underexplored (Bardgett, Mommer, & De Vries, 2014), due in large part to the relative difficulty in obtaining and processing large numbers of samples (however, see the root trait data bank FRED; Iversen et al., 2017). Like leaf traits, root traits may also indicate different axes of plant ecological strategies but several studies now point towards a multi-dimensional interpretation of below-ground traits (Kramer-Walter et al., 2016; Weemstra et al., 2016), where some traits may respond in coordination with above-ground (such as root tissue density in the case of trees), while others, such as SRL, may not.

4.4 | ITV and predictive ecology

Traits are increasingly being incorporated into macro-scale studies and used to make predictions about future community composition (Laughlin et al., 2012; Suding et al., 2008), notably within the theoretical corpus of functional biogeography (Violle et al., 2014). We observed differences in range-wide ITV even among our small group of ubiquitous species. Each species was characterized by different partitioning of variance across scales and between analogous traits. Our results highlight species-specific idiosyncrasies that might arise when inferring ecological processes from traits measured on different plant organs (Shipley et al., 2016; Violle et al., 2007), underscoring the need for research on strategies (e.g. Violle et al., 2007; Wardle et al., 2009; Garnier et al., 2015; Kumordzi et al., 2016) as well as the need for synthesis to identify suites of traits that are related to particular ecosystem processes (Aubin et al., 2016; Pérez-Harguindeguy et al., 2013).

Our results signify that there is more than one strategy to achieve a ubiquitous presence in forest understorey plant communities. Species can be effective colonizers able to establish over a wide range of environmental conditions, or they can maintain their presence in the understorey through vegetative regeneration and a high level of plasticity in response to canopy opening (Aubin et al., 2005; Gilliam & Roberts, 2003; Rowe, 1983), or perhaps both. These different strategies among species could directly influence the ability of entire communities to adapt or shift under climate change. "Winner" species under climate change may consequently not only be species that display traits we expect to be favoured, but may also be those

possessing large ITV. By necessity, our study focused only on a small group of species, but greater ITV in more acquisitive species warrants further research.

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AUTHORS' CONTRIBUTIONS

I.A., F.C. and A.D.M. designed methodology. I.A., B.S., J.J., F.C., M.A., A.A., W.B., Y.B., I.B., M.B., L.d.G., S.D., N.F., D.G., S.E.M., B.H., M.H., F.H., N.I., A.M., A.M., J.M., C.M., D.M., N.T., J.P.T. and A.D.M. collected the data. B.B.K., I.A., B.S. and A.D.M. conceived the ideas and analysed the data. B.B.K., I.A., F.C., C.V. and A.D.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <http://doi:10.5061/dryad.434gv5p> (Kumordzi et al., 2019).

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