

Understanding context dependence in the contribution of intraspecific variation to community trait–environment matching

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Abstract. Intraspecific trait variation (ITV) plays a potentially important role in determining functional community composition across environmental gradients. However, the importance of ITV varies greatly among studies, and we lack a coherent understanding of the contexts under which to expect a high vs. low contribution of ITV to trait–environment matching among communities. Here we first elaborate a novel conceptual framework posing specific hypotheses and predictions about the environmental and ecological contexts underlying the contribution of ITV to community trait turnover. We then empirically test these predictions in understory herbaceous plant communities in a montane environment, for three functional traits (flowering phenology, specific leaf area, and height). We found that different components of trait variation mapped onto different environmental axes, specifically reporting a greater contribution of ITV along non-climatic axes (e.g., soil properties, light) than along the main climatic axis (i.e., elevation), as predicted by the hypothesis that phenotypic plasticity (a major source of ITV) is greatest in response to conditions varying at a small spatial scale. Based on a variant of the niche-variation hypothesis, we predicted that the importance of ITV would be greatest in the lowest-diversity portion of the elevational gradient (i.e., at high elevation), but this prediction was not supported. Finally, the generally strong intraspecific responses to the gradient observed across species did not necessarily give rise to a high contribution of ITV (or vice versa) given (1) an especially weak or strong response of a dominant species driving the community-level trend, (2) differences among species in the direction of trait–environment response cancelling out, or (3) relatively narrow portions of the gradient where individual species abundances were high enough to have an important impact on community-level trait means. Our research identifies contexts in which we can predict that local adaptation and phenotypic plasticity will play a relatively large role in mediating community-level trait responses to environmental change.

Key words: community ecology; elevation; environmental gradients; intraspecific variation; plant functional traits; species turnover; trait–abundance–environment relationship.

INTRODUCTION

Consideration of functional traits has improved our understanding of the selective pressures constraining community assembly across environmental gradients (Violle et al. 2007). As a given set of environmental conditions favors some functional strategies over others, individuals are filtered in a community based on their physiological, morphological, and phenological traits. The functional composition of communities may therefore change with environmental conditions as the mean and range of trait values admitted by the filter varies across the gradient (Díaz et al. 1998, Cornwell and Ackerly 2009). Understanding the processes underlying trait–environment “matching” is thus key to predicting the nature and magnitude of changes in ecosystem function under environmental change (Sandel et al. 2010, Laughlin et al. 2012).

Trait–environment matching can be maintained by adaptive trait variation occurring at two levels: among and within species (Ackerly 2003). First, local environmental conditions will select among species based on their average trait values such that species turnover (SPT) will contribute to trait–environment matching along the environmental gradient (Weiher and Keddy 1995). Second, individuals within species might express different trait values in different environments (i.e., intraspecific trait variation, ITV), either due to phenotypic plasticity or genetically-based local adaptation (Cody and Mooney 1978, Sultan 1987). Partitioning the relative importance of these processes along a spatial gradient of interest can constitute a basis for predicting the rate and mechanisms underpinning functional community responses to temporal environmental change (Davis et al. 2005). A large importance of SPT to community-level trait turnover indicates that maintaining trait–environment matching under temporal environmental change will require that dispersal allows species to spatially track their environmental optima (Parmesan 2006). In contrast, a large contribution of

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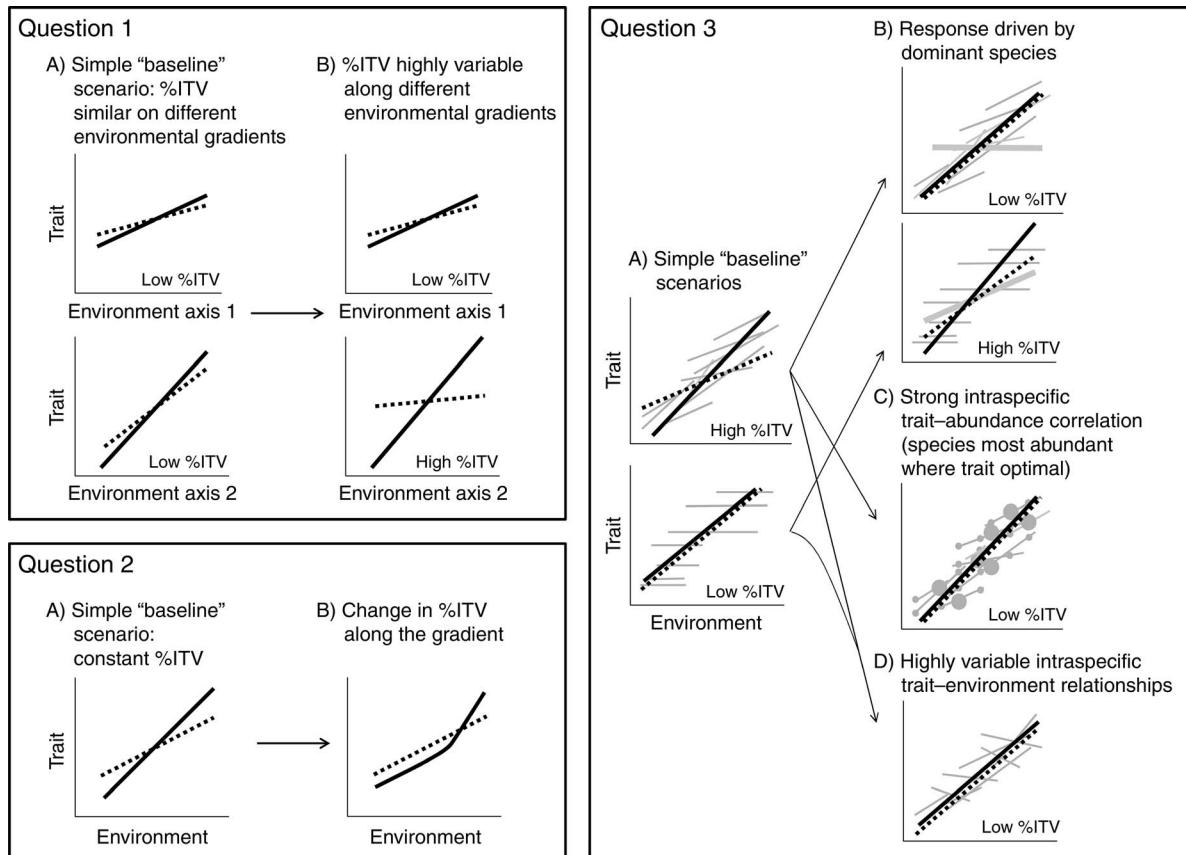


FIG. 1. Different pathways to detecting low or high relative contributions of intraspecific trait variation (ITV) to trait-environment matching. Heavy black lines represent relationships for community weighted trait means including (solid) or excluding (dotted) ITV. The difference in slopes represents the contribution of ITV to trait-environment matching. Gray lines represent trait variation within individual species, with the most abundant species represented by the thick line. The size of the dots in Question 3, panel (C) are proportional to the local relative abundance of the species. For each of the main questions in this paper (1–3), panel (A) represents the baseline scenario (Cornwell and Ackerly 2009), while panels (B–D) represent alternative scenarios that can lead to important changes in the detected contribution of ITV to community trait turnover.

ITV indicates a greater importance of in situ adaptive responses of resident species to environmental change, which may occur rapidly (plasticity) or over the course of multiple generations (adaptive evolution; Jump and Peñuelas 2005, Reed et al. 2010).

Recent studies report a potentially important role for ITV in determining functional community composition (Albert et al. 2011, 2012). For example, Jung et al. (2010) detected statistical signatures of environmental filtering and niche partitioning more strongly when taking into account ITV. Similar support for a significant role of ITV in mediating community assembly across gradients comes from studies using population-level trait data (rather than species-level means) for detecting trait-environment relationships among communities (Cornwell and Ackerly 2009, Leps et al. 2011, Sundqvist et al. 2011). Recent studies have led to a better understanding of the contribution of ITV to functional diversity across levels of biological organization and geographical scales (Albert et al. 2010, 2011, 2012), although the contexts in which one would expect a high

or low contribution of ITV to trait turnover along gradients remain nebulous, partly due to the paucity of studies having reported such results. For example, Cornwell and Ackerly (2009) attributed 14% of community-level variation in specific leaf area (SLA) to ITV along a moisture gradient in chaparral communities, while Jung et al. (2010) reported a contribution reaching 44% for the same trait and type of gradient in wetlands.

Here we develop a novel conceptual framework (Fig. 1) to investigate the sources of plant community trait turnover along environmental gradients. In a montane environment, we test how the contribution of ITV varies according to (1) the different environmental axes under consideration, (2) the segment of the environmental axis considered, and (3) the structure of species functional responses to the gradient. More specifically, we examine for question 3 (a) the role of dominant species, (b) the nature of trait-abundance relationships within species along the gradient, and (c) covariation among species in the direction of their trait response to the environment. The conceptual framework in Fig. 1 presents predictions

of the scenarios in which one would expect either a low or a high contribution of ITV.

Hypotheses and predictions

Most studies reporting both community-level and species-level functional responses to environmental variation have compared these responses along single environmental axes, such as aridity (Cornwell and Ackerly 2009, Jung et al. 2010) or productivity (Richardson et al. 2005, Sundqvist et al. 2011). When considering several environmental axes, studies have otherwise reported trait–environment correlations for each level of trait change separately (within each species, and among species mean traits) along each axis (Andersen et al. 2012, Kröber et al. 2012; but see Leps et al. 2011). However, it is unclear whether we should expect the importance of ITV to trait–environment matching to be the same along different environmental axes, even within the same system (Fig. 1, Question 1). The answer to this question has important implications for predicting community trait turnover in response to multivariate environmental change.

We hypothesize that discrepancies between the environmental drivers of SPT and ITV may result from differences in the spatial scale of heterogeneity between environmental factors, and the evolutionary and ecological consequences of such differences. Specifically, for an environmental factor varying predominantly across large spatial scales, long-term barriers to gene flow or a high cost of plasticity might restrain the adaptive capacity of species (Sultan and Spencer 2002), and as such prevent ITV from making an important contribution to trait–environment matching. We thus expect lineage diversification to historically have occurred along such niche axes, leading to an important role for species turnover in maintaining trait–environment matching along such gradients in the present day. In contrast, small-scale heterogeneity is expected to select for plasticity within species (Levins 1969, Baythavong 2011), such that ITV might play a large role in trait–environment matching along such gradients. In our region of eastern North America, climate varies predominantly over large scales (i.e., thousands of kilometers), and even in montane areas climate is relatively constant within the range of typical dispersal distances (<10 m) for understory plants (Cain et al. 1998). In contrast, non-climatic factors in the forest understory (our study system), such as soil properties and light, show tremendous variation at the scale of meters or centimeters (Canham et al. 1990, Bell et al. 1993). As such, we predict that the relative importance of species turnover to trait–environment matching will be maximized along the elevational gradient (strongly correlated with temperature), while the role of ITV will be greatest along axes such as light and soil nitrogen.

Differences across studies in the contribution of ITV to community-level trait–environment matching along a given gradient (e.g., Cornwell and Ackerly 2009, Jung et

al. 2010) suggest that community context itself may influence the contribution of intraspecific processes (Fig. 1, Question 2). Changes in the relative importance of ITV along an environmental axis within a single study system have, however, not been investigated. We here hypothesize that ITV should play a greater role in harsh environments (high elevation in our case) where lower species diversity might lead to greater expression of ITV in those species able to pass the filter (the “niche variation hypothesis”; Van Valen 1965, Bolnick et al. 2011, Emery and Ackerly 2014).

Variation in the direction and strength of species’ trait and abundance responses to a gradient and its impact on the contribution of ITV to community trait turnover has seldom been examined. A commonly-used conceptual framework (Fig. 1, Question 3A; Cornwell and Ackerly 2009) suggests that the response of the most abundant species is representative of others, with no explicit consideration of abundance–environment relationships. However, very different results can be obtained when using abundance-weighted vs. unweighted trait means (Kichenin et al. 2013), calling into question this assumption (Fig. 1, Question 3B, C). Also, several studies report interspecific variation in the direction of trait–environment slopes along the same gradient (Albert et al. 2010, Kichenin et al. 2013, Mayor et al. 2014), suggesting contrasting contributions of different species to community-level turnover. In this case, the role of ITV can appear minimal, despite strong species-specific trait–environment responses (Fig. 1, Question 3D).

Here we address these questions by assessing trait–environment associations in herbaceous plant communities across a mountainside in southern Quebec (Canada). Our environmental gradient spanned deciduous (low elevation) to coniferous (high elevation) forest, with individual plots varying substantially according to environmental variables such as climate, light, and soil conditions. To comprehensively examine the structure of ITV across gradients, we sampled traits at the population (i.e., plot) level in every species present in our communities, considering three major axes of functional strategies: peak flowering date, specific leaf area, and vegetative height.

METHODS

Study site

Mont-Mégantic National Park (45°27′21″ N, 71°09′08″ W) is a 55-km² protected area located in southern Quebec, Canada, on the northern edge of the Appalachian Mountain range (see Plate 1). The climate is humid continental at low elevation (~500 m above sea level) shifting to a boreal-subarctic climate at high elevation (up to ~1100 m). Mean annual temperature decreases 0.64°C per 100 m of elevation, shifting from 3.6°C to 0.4°C along the mountainside, consequently reducing the length of the growing season from ~100 days to ~80 days (Graillon et al. 2007). Tree vegetation

in the park is characterized by an altitudinal gradient from maple-yellow birch stands at low elevation to balsam-fir-red-spruce stands at high elevation (Savage and Vellend 2014). Our study site consists of the east-facing slope of Mont-St-Joseph ($\sim 3 \text{ km}^2$), one of the crest mountains along which this vegetation gradient is especially evident (Brown and Vellend 2014).

Plot establishment and environmental monitoring

Along each of three transects, we established 10 4×26 m plots (104 m^2), perpendicular to the elevational gradient, at ~ 40 -m elevation intervals (30 plots in total). We selected upland sites under tree cover to limit the influence of wet areas, large gaps, and succession on vegetation patterns. During the growing seasons of 2012 and 2013, we visually estimated percent cover (“local abundance”) of each herbaceous species at each plot. Our species pool included both ephemeral and summer-flowering species of herbaceous angiosperms and shrubs reaching ≤ 1 m at maturity, as well as pteridophytes. At each plot, we measured environmental variables thought to influence plant trait variation: elevation, air temperature, slope, canopy openness, soil depth, and nine soil physicochemical characteristics (details in Appendix A).

Trait selection and measurement

Three functional traits were selected to represent major axes of adaptive plant strategies. Specific leaf area (SLA) is the one-sided area of a fresh leaf divided by its oven-dry mass and tends to be correlated with photosynthetic rates (positively) and leaf life-span (negatively), reflecting a trade-off between resource capture and conservation (Reich et al. 1994). Maximum foliage height is the distance between the ground and the highest photosynthetic tissue and determines access to light (Givnish 1982). Reproductive phenology represents the timing of reproductive development (Inouye 2008). We measured phenology of all angiosperms as peak flowering date, the date at which most flowers are open in a population.

For assessing both SLA and maximum vegetative height, we haphazardly selected within a 5-m margin of each plot five non-reproductive individuals of every species recorded within the plot (details in Appendix A). For estimating SLA (see Pérez-Harguindeguy et al. 2013), one healthy leaf of each selected individual was collected without petiole, digitally scanned, and its area determined using ImageJ (Rasband 1997–2014). Leaves were then dried at 60°C for 72 h before weighing. Height of every individual was measured in the field to the nearest centimeter using a measuring tape. For analyses, SLA was log-transformed to meet the assumption of normality.

We assessed flowering phenology in 2013. This was done in a subset of plots given the labor-intensive nature of phenological observations. On each of two transects, we monitored the number of open flowers of all species every three to five days from April to September in six

plots spanning evenly the mountainside. Peak flowering date was estimated by optimizing a Gaussian function over the flowering density curves of each species at each site, and extracting the mean of the distribution. The total number of flowering stems per species was recorded at each flowering census, and the relative abundances of species in the “flowering community” were calculated as the number of flowering stems of a species at its peak flowering date divided by the total number of flowering stems (at peak flowering) across all species. Further analyses of phenology were performed from this flowering community.

Statistical analyses

Drivers of trait–environment matching among communities.—From an initial set of 13 environmental variables, we extracted a set of five showing minimal collinearity for use in subsequent analyses: elevation, slope, canopy openness, total inorganic nitrogen concentration (extractable $\text{NH}_4^+ + \text{NO}_3^-$), and a soil acidity axis (details in Appendix A).

We quantified the relative importance of ITV and SPT in determining the total trait variation along an environmental axis using the variation partitioning method of Leps et al. (2011) adapted by Kichenin et al. (2013) for application to continuous gradients. This method consists of three steps. First, for each plot j , we computed three types of community weighted means ($\text{CWM}_{\text{SPT+ITV}}$, CWM_{SPT} , CWM_{ITV}). $\text{CWM}_{\text{SPT+ITV}}$ was calculated from the trait values measured locally for each population of each species occurring in that plot, CWM_{SPT} from the mean trait values of each of these species, and CWM_{ITV} as the difference between the two. While variation among $\text{CWM}_{\text{SPT+ITV}}$ values across an environmental gradient involves both SPT and ITV, CWM_{SPT} and CWM_{ITV} only account for SPT and ITV, respectively. We used plot-scale relative abundances as a weighting factor: vegetative percent cover for SLA and height, and proportion of flowering stems at peak flowering date for phenology.

Second, we performed separate regressions of each of the three CWMs on each environmental variable, and obtained the total and the regression sums of squares. For each combination of trait and environmental axis (E), three separate models of trait–environment associations were then obtained, the first accounting for both interspecific and intraspecific sources of variation ($\text{CWM}_{\text{SPT+ITV}} \sim \text{E}$), the second accounting only for SPT ($\text{CWM}_{\text{SPT}} \sim \text{E}$), and the third accounting only for ITV ($\text{CWM}_{\text{ITV}} \sim \text{E}$). Regressions were performed using both linear and quadratic models for all trait–environment combinations. If adding the quadratic term for a given variable resulted in a significantly better model fit for any one of the three models (using F tests), we used the quadratic term for that variable in all three models. This decision was made independently for each trait–environment combination.

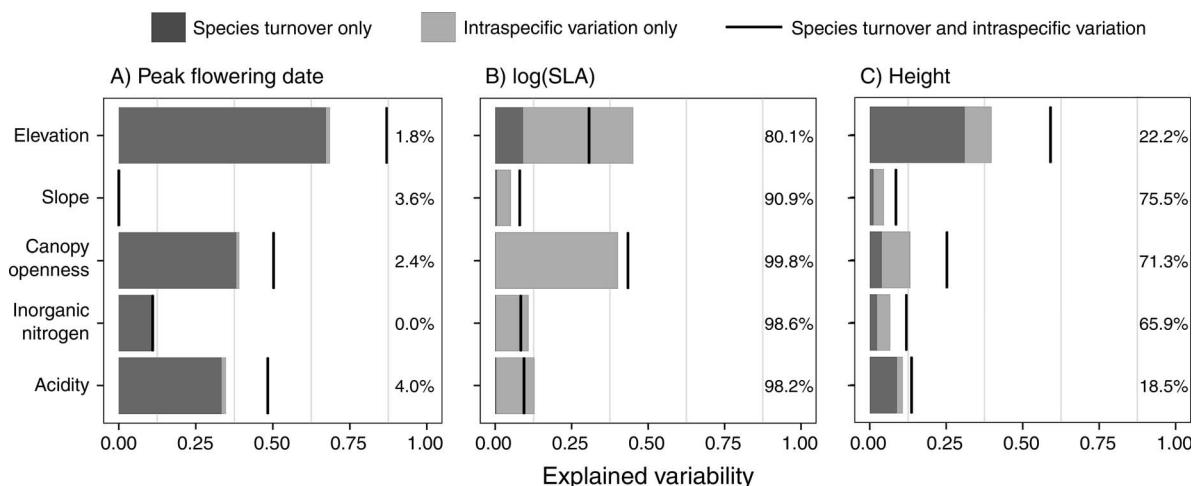


FIG. 2. Partitioning intraspecific and interspecific sources of trait variation along environmental gradients. Explained variability of trait–environment relationships are presented for each of three traits, as predicted by five different environmental variables (see Appendix C for details including statistical significance) for (A) peak flowering date, (B) specific leaf area (SLA), and (C) height. Lines indicate the amount of variability explained by both interspecific and intraspecific (i.e., total) variation. Dark gray portions of bars represent the variability of the total model explained by species turnover (SPT) only; pale gray portions represent the variability of the total model explained by ITV only. The space between the end of the bar and the black line represents covariation between the interspecific and intraspecific components of trait change (positive if the black line is further to the right than the stacked bars, and vice versa). Numbers on the right indicate the relative importance of ITV to community trait turnover for that environmental axis, calculated from simple regression models as $SSR_{ITV}/(SSR_{ITV} + SSR_{SPT})$, where SSR is the regression sums of squares.

Third, the variance in CWM attributable to SPT and to ITV (*absolute* explanatory power) was assessed as the ratio between the regression sum of squares of the SPT model (SSR_{SPT}) or the ITV model (SSR_{ITV}), respectively, and the total sum of squares of the model including both components ($SST_{SPT+ITV}$). The importance of ITV relative to SPT (*relative* explanatory power) was calculated as $SSR_{ITV}/(SSR_{SPT} + SSR_{ITV})$, representing the ratio of the explanatory power of ITV relative to the portion of total variation explained by the two components together.

In order to assess whether SPT and ITV were best explained by the same gradients, we calculated the individual contribution of each environmental variable to multiple regression models conducted individually for each component of trait change (total, SPT and ITV), including all environmental variables as predictors (details in Appendix D).

Relative importance of ITV along the gradient.—Given that elevation was the best predictor of total turnover for all traits, we focused subsequent analyses on trait–elevation relationships. To test whether the relative importance of ITV changed along the elevational gradient, we repeated the same variation partitioning analysis described in *Drivers of trait–environment matching among communities* within sliding windows of five plots along each transect. We then estimated the slope of the linear relationship between the relative importance of ITV and the mean position of the window on the gradient. Given that data points were not independent, we tested for significance of this relationship by

permutation, by randomly swapping $CWM_{SPT+ITV}$ and CWM_{SPT} at each site, then recalculating contributions of ITV to obtain a new slope value for this relationship. The observed slope value was compared to those obtained with 999 such permutations.

Pathways to high or low relative importance of ITV.—The impact of (1) the dominant species (Question 3B, see Fig. 1), (2) intraspecific trait–abundance relationships (Question 3C), and (3) variation in the direction of intraspecific trait–environment slopes (Question 3D) on %ITV was assessed by comparing the observed %ITV to (1) that obtained by first removing the most abundant species from the analysis, (2) those calculated after randomizing intraspecific abundances within each species' distribution along the gradient (9999 permutations), and (3) that obtained by forcing all intraspecific trait–environment slopes to be in the same direction. Details are presented in Appendix E for (2) and (3).

RESULTS

Drivers of trait–environment matching

We recorded 51 herbaceous species in total, 30 of which were flowering in at least one of the 12 sites where phenology was recorded. For all three traits, variation among plots in CWMs (all sources of variation combined) was best explained by elevation (Fig. 2). The mean date of peak flowering of communities was positively associated with elevation, while variation in SLA and height followed unimodal relationships, being respectively lowest and highest at mid-elevation (Fig. 3A–C, statistics summary in Appendix C). Canopy

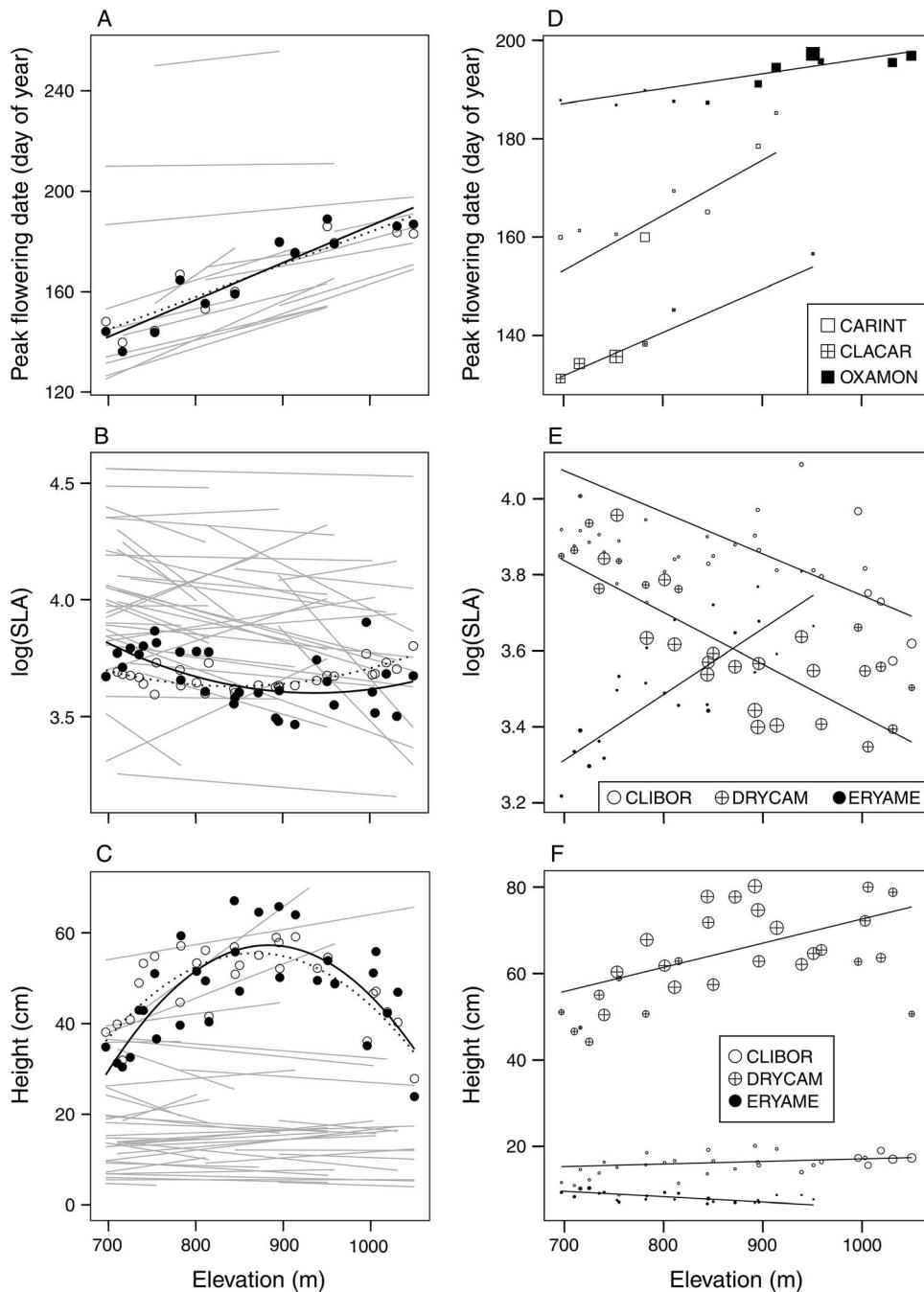


FIG. 3. Relationships between trait variation and elevation (A–C) among communities and (D–F) for the most abundant species. In (A–C), each pair of points sharing the same position along the gradient represents a plot. Filled circles and solid lines represent the community weighted means (CWMs) calculated with plot-level trait values (i.e., including ITV), and open circles and dotted lines represent those calculated with species-level trait means (i.e., excluding ITV). Gray lines show linear responses of each species occurring in at least four plots for visual purposes; the statistical analyses used for calculating community trait turnover made no assumptions about the shape of these relationships (see *Material and methods: Statistical analyses* for details). In (D–F), each point represents a population within one of three selected species, chosen from the six most abundant in each case to minimize overlap in points. Each species is represented by a different symbol, the size of which is proportional to the species' relative abundance within a site: *Carex intumescens* (CARINT), *Claytonia caroliniana* (CLACAR), *Oxalis montana* (OXAMON), *Clintonia borealis* (CLIBOR), *Dryopteris campyloptera* (DRYCAM), and *Erythronium americanum* (ERYAME). The most abundant species differ between phenological (D) and vegetative (E, F) traits, since the most abundantly flowering species did not necessarily have the highest percent cover at a given site. SLA was measured as cm^2/g .

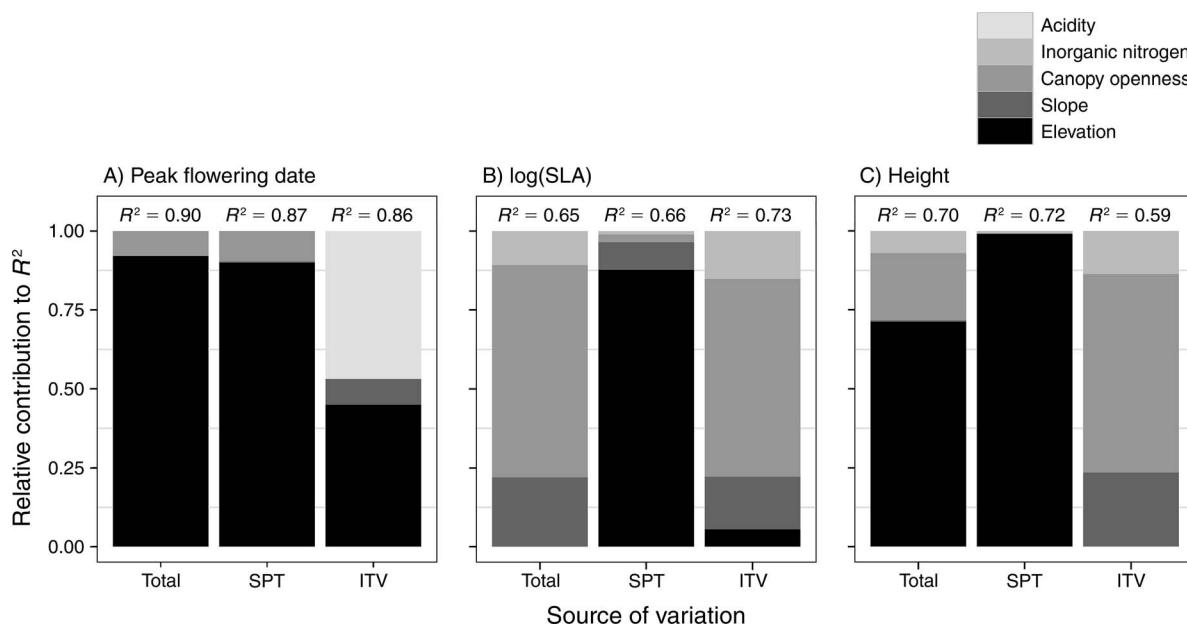


FIG. 4. Relative contributions of five environmental factors to explaining variability in total, interspecific, and intraspecific trait variation. The relative contribution of each environmental factor to explaining variation in a multiple regression model including both first-order and second-order terms is illustrated for each component of trait variation, per trait. The total R^2 of each multiple regression model is indicated on top of each column.

openness and acidity also explained considerable variation in all traits; soil nitrogen and slope did not (Fig. 2).

The relative importance of ITV differed among traits, being highest for SLA and lowest for phenology along any given environmental gradient (Fig. 2). For example, ITV accounted for 80.0% of the SLA–elevation relationship, but only 22.2% of the height–elevation relationship and 1.8% for peak flowering date vs. elevation (Fig. 2). The contribution of ITV to total variation in any trait further varied depending on the environmental axis in question (Fig. 2, Fig. 4): ITV was consistently better predicted by non-climatic environmental variables such as canopy openness and acidity, while SPT (regardless of trait) was mostly explained by elevation.

Positive covariance between SPT and ITV was observed for most trait–environment combinations, indicating that these effects reinforce each other in maintaining the association between traits and environment. The vertical black lines in Fig. 2 are thus most often further to the right than the sum of grey and black bars (see Leps et al. 2011). Only for SLA along elevation did the SPT and ITV components of community trait turnover covary negatively, as a result of the concurrent increase in species mean SLA and decrease in the average intraspecific response in the upper half of the gradient (see Fig. 3).

Relative importance of ITV along the gradient

The relative importance of ITV did not vary significantly with elevation for height (Appendix B). A

weak negative trend between the relative magnitude of intraspecific effects and elevation was observed for SLA, although it resulted from an increase in the interspecific component of trait change rather than a change in the magnitude of explained variation of ITV (Appendix B).

Pathways to high or low relative importance of ITV

The impact of the most abundant species on the contribution of ITV to community-level trait–environment relationships (%ITV) differed among traits. The flowering and vegetative communities were respectively dominated by *Oxalis montana* (28.0% of all flowering stems recorded), and by *Dryopteris campyloptera* (66.0% of all vegetative cover). As *O. montana* had a shallower slope between peak flowering date and elevation than the species average, removing it from trait–environment analyses resulted in a modest increase in %ITV (Table 1). In contrast, *D. campyloptera* was one of the most variable species for both SLA and height (steep slopes with elevation), such that removing it resulted in a substantial decrease in %ITV.

Intraspecific trait–abundance–environment relationships also contributed to decreasing the relative importance of ITV in all traits across the elevational gradient. The observed %ITV was significantly lower than %ITV calculated after randomizing abundances among plots (within species). This result is expected when abundance within species is highest in the subset of sites where trait values most closely match the site average (as illustrated in Fig. 3D–F).

TABLE 1. The contribution of intraspecific trait variation (ITV) to community trait turnover (%ITV) in analyses of the full data set (Observed), and in analyses of data sets modified in order to address Questions 3B–3D (see Fig. 1).

Trait	Observed %ITV	Question		
		3B) %ITV with most abundant species removed	3C) %ITV with abundances randomized within species	3D) %ITV with intraspecific slopes forced to be in the same direction
Peak flowering date	1.8	4.9	17.0 ($P = 0.0079$)	1.8
log(SLA)	80.0	36.7	98.1 ($P = 0.0002$)	84.6
Height	22.2	0.1	74.7 ($P = 0.0009$)	29.6

Notes: Question 3C was addressed using a null model (see Appendix E), allowing calculation of whether the difference from observed %ITV was significant. For this question, mean %ITV of all randomizations is reported in the table, with P values in parenthesis. SLA, specific leaf area.

The direction of intraspecific trait responses to the elevation gradient was consistent among species for peak flowering date, with all species flowering later at higher elevations (Fig. 3A). However, for both SLA and height, the direction of trait–elevation relationships was variable among species (Fig. 3B, C), with negative slopes found in 25 out of 34 species for SLA, and 18 out of 34 for height. Forcing all intraspecific trait–elevation slopes to have the same directionality (negative for both SLA and height) increased %ITV by 4.6% and 7.4%, respectively (Table 1), suggesting that interspecific variation in the direction of trait–environment slopes reduces the effect of ITV on community trait turnover, albeit to a lesser degree than the dominant species.

DISCUSSION

We have elaborated a novel conceptual framework (Fig. 1) and presented empirical evidence demonstrating the multiple pathways to a low or high contribution of ITV to community-level trait turnover. By taking a multivariate environmental approach, we have gone considerably further than previous studies in showing that different components of trait variation (intraspecific vs. interspecific) mapped onto different environmental axes. We also presented one of the first analyses partitioning community-level trait change in moving windows along an environmental gradient, although we found little evidence for a change in the relative importance of ITV with elevation, contrary to our prediction. Finally, we showed how the structure of individual species' responses determined the contribution of ITV to community trait turnover. Specifically, strong trait–environment relationships within species did not necessarily lead to a high relative importance of ITV (or vice versa) because (1) the contrasting functional response of a dominant species alters community-level trait–environment associations drastically, (2) opposing intraspecific trait–environment slopes cancel out, or (3) most species are sufficiently rare in suboptimal environmental conditions that intraspecific trait–environment relationships contribute very little to abundance-weighted community trait variation.

Environmental drivers of trait variation along a mountainside

The contribution of ITV to community-trait–environment matching differed among traits, as has been previously demonstrated (Jung et al. 2010, Leps et al. 2011, Kichenin et al. 2013), but also among environmental axes for each trait (Fig. 2). This result was notably a consequence of discrepancies in the environmental drivers of species turnover (SPT) and intraspecific trait variation (ITV). As predicted, SPT was greatest along the elevation gradient, while ITV was best predicted by non-climatic factors, particularly canopy openness (Fig. 4). Among the few studies reporting comparable results, Dwyer et al. (2014) also found differences among environmental gradients best predicting SPT and ITV in SLA: the contribution of ITV was greatest along axes of woody plant cover, nitrogen, and pH, and least along axes of soil phosphorus and residual dry grass matter. Similarly, Leps et al. (2011) reported more variation in community mean SLA explained by ITV along a fertilization gradient than a mowing one. Consistent with our hypothesis, these results suggest that the eco-evolutionary drivers of trait variation may be different within and among species, indicating that environmental variables varying over potentially larger scales (climate and productivity) may determine SPT more than ITV. Global environmental change is fundamentally multivariate, with climate, nutrients and disturbance (among other factors) typically all changing in concert (Dale et al. 2000, Lewis et al. 2004). Our results suggest a greater role of ITV in underlying community responses to canopy gaps, while responses to changes in climate, at least over the long term, should be dominated by species turnover.

Relative importance of ITV along the gradient

We detected no trend in the relative importance of ITV with elevation for height (Appendix B). For SLA, contrary to expectations, the contribution of ITV to community trait turnover decreased with increasing elevation (and therefore decreasing species richness), although the trend was weak (Appendix B). However, this resulted largely from an increase in the magnitude of



PLATE 1. Transition from deciduous to coniferous forest across an elevational gradient at Mont-Mégantic National Park, Quebec, Canada. Photo credit: G. Lajoie.

interspecific effects along the gradient, rather than from a decrease in raw intraspecific effects (Appendix B). Therefore, instead of lower levels of competition enhancing the expression of ITV at high elevation (Van Valen 1965, Bolnick et al. 2011), we can speculate that stronger environmental filtering at harsher high-elevation sites might lead to higher species turnover across the gradient, as several species cannot survive and are thus excluded from the species pool at these elevations. An increase in species turnover in herbaceous plant communities has also been observed by Itow (1991) along an elevational gradient. Future studies evaluating context dependence in the importance of ITV to community-level trait–environment matching would benefit from increasing gradient length and sampling density, so as to increase the power to detect trait–environment associations across environmental gradients.

Pathways to high or low relative importance of ITV

The nature of trait–abundance relationships within and among species along the elevational gradient determined the extent to which ITV played a role in maintaining trait–environment matching, as depicted in our conceptual framework (Fig. 1). Species varied not only according to the strength of trait–environment relationships, but also in the direction of these relationships (Fig. 3A–C, Table 1). Idiosyncrasies in species responses to gradients have been reported (e.g., Albert et al. 2010, Sundqvist et al. 2011, Kichenin et al. 2013), though their influence on the contribution of ITV to

community trait turnover had not been discussed (Vellend et al. 2014). For SLA and height, contrasts between species responses (Fig. 3B, C, Table 1) are suggestive of interspecific variability in the functional strategies apt to maintain fitness along the elevational gradient, which may result from species either responding to different environmental variables covarying with elevation (e.g., Janousek and Folger 2013), or experiencing different micro-environmental conditions than those captured by plot-level averages (e.g., Roscher et al. 2011). To the extent that intraspecific trait responses to the environment are adaptive, the importance of ITV in maintaining trait–environment matching might therefore be underestimated when species have contrasting responses, although the difference here (5–7%) was relatively small.

More striking was the major impact of the strength of the trait–environment relationship in the most abundant species on the contribution of ITV to community trait turnover, particularly for SLA and height (Table 1). Thus, we cannot assume that the direction and strength of trait–environment relationships of dominant species are representative of the broader set of species. Differences in the impact of the most abundant species among traits might also be due partly to the greater average relative abundance of the dominant species in the vegetative community (*Dryopteris campyloptera*, 66%) than in the flowering community (*Oxalis montana*, 28%). For SLA and height, the trait–environment relationship was especially strong in the most abundant species (*D. campyloptera*), which thereby enhanced an

already large contribution of ITV (Fig. 2). We can thus expect *D. campyloptera* to play a major role in maintaining community trait–environment matching in the future if (1) the costs of plasticity or adaptation are low and (2) the strength of trait–environment relationships across space is indicative of likely trait responses to environmental change across time (Almeida et al. 2012).

In contrast to the vegetative traits, the low contribution of ITV to the peak flowering date–elevation relationship was underlain by low ITV in the most prolific flower-producing species, *O. montana* (Fig. 3D). Still, even in the absence of this species, the contribution of ITV was small (Table 1) given the strong tendency for species to make important contributions to the local flowering community only in a narrow portion of their distributions (Fig. 3D). As such, we can predict that future responses of community-level flowering time to climate warming will be dominated by species turnover, at least over the long term. Strong trait–abundance correlations in all three traits (Table 1) suggest that temporal species turnover would not only involve changing species identity but also changes in the relative abundances of species with different trait values.

In sum, we have demonstrated that the contribution of ITV to community trait turnover depends on the environmental axis considered, on variation among species in the direction and strength of trait–environment relationships, and the presence or absence of strong peaks in species abundance along a given gradient. Careful examination of species functional responses underlying community-level patterns of variation in a multivariate environmental framework appears essential to assessing the role of ITV in community assembly, and to predicting community-level trait responses to environmental change.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/15-0156.1.sm>