

# Intraspecific Trait Variability Determines Understorey Plant Community Assembly

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## Research Article

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# Abstract

Increasing evidence points to the major impact of intraspecific variability in species characteristics on community assembly. Contrasting theories predict that high trait variability might either steepening dominance orders or promote diversity. Here, we try to test these predictions with understorey plants in a Polish mixed temperate forest.

We focus on four important traits (leaf dry mass LDW, plant height SH, specific leaf area SLA, and number of flowers  $N_F$ ) of the small balsam *Impatiens parviflora*, the dominant species in this forest system. We relate trait variability to community species richness and abundances, as well as to soil characteristics.

The variance – mean relationships of LDW, LH, and  $N_F$ , but not of SLA, closely followed power functions with slopes  $> 1.5$ . Contrary to theory, abundances but not species richness of non-*I. parviflora* species significantly decreased within increasing variance in *I. parviflora* trait expression. High trait variability prevailed a higher species richness. Trait variability did not significantly influence species composition and was not significantly correlated with soil characteristics. Our results emphasize the need to study trait variability in terms of appropriate statistical standards as provided by the allometric variance - mean relationship. We argue that an individual based study of local trait variability might return important insights into the composition and assembly of local communities.

## Introduction

Traditionally, studies on plant community assembly have been species centred (Götzenberger et al. 2012) focusing on three important processes, dispersal, competition, and habitat filtering (Callaway and Walker 1997; Maire et al. 2012; Ulrich et al. 2016). This work revealed major habitat dependent trade-offs between these drivers (D'Amen 2018). Additionally, the spatial distribution of individual plants was found to affect competitive interactions and to increase community stability (Ives 1991; Stoll and Prati 2001). However, species based approaches have well-known shortcomings as they do not cover intraspecific trait and niche differences (Jung et al. 2010), and might lack generality beyond the focal community (Zakharova et al. 2019).

Trait-based approaches overcome part of the limitations of species based approaches and are increasingly used to study community assembly (McGill et al. 2006; Viole et al. 2007; Zakharova et al. 2019). They allow for a direct assessment of competitive interactions at the niche level and cover intra- and interspecific variability of important species traits (e.g. Blonder 2017). However, most work on plant niche overlap has been done with literature data using averaged trait values (e.g. Schellenberger Costa et al. 2018; Kubota et al. 2018; Kermavnar and Kurnar 2020). This work has revealed complex and site specific relationships between the effects of niche and environment, both triggering species co-occurrences (Bar-Massada 2015).

Increasing evidence points to the major impact of intraspecific variability in species characteristics on community assembly (e.g. Jung et al. 2010; Bolnick et al. 2011; Siefert et al. 2015; Hausch et al. 2018). Theoretical studies predict major effects of intraspecific variability on various ecological processes (cf. Bolnick et al. 2011; Westerland et al. 2021). The trade-off of intra-and interspecific variability in key traits have been identified to determine the probability of local plant competitive success and persistence (Carlucci et al. 2015). Intraspecific trait variation has also been shown to influence the spatial distribution of conspecifics (De Rosches et al. 2017) and heterospecifics (Hart et al. 2016; Hausch et al. 2018) and thus might influence local community assembly (Jung et al. 2010). Therefore, trait variation might be an important trigger of local community assembly (Carlucci et al. 2015) and consequently species interactions and diversity (Westerland et al. 2021).

In general, we might analyse sources of intraspecific trait variability from the endpoints of a stochastic – deterministic gradient. The stochastic endpoint includes, for instance, the genetic diversity or phenotypic plasticity, partly reflecting random environmental variation (Forsmann 2015). On the other side, average trait expression might change deterministically along ecological gradients, particularly environmental (Violle et al. 2007). In the latter case the distribution of traits with respect to ecological drivers should be not random. For example, Jung et al. (2010) reported predictable intraspecific changes of grassland plant specific leaf area (SLA) but not of leaf dry weight (LDW) along flooding gradients. As both traits exhibited significant intraspecific variability, we might interpret the contrasting results in terms of individual plasticity and reaction to changing environmental conditions. Henn et al. (2018) argued that high phenotypic plasticity enables alpine plants to persist within communities and to cope with changing environmental conditions. These and other studies (e.g. Hausch et al. 2018; Sandel et al. 2021) were done along marked environmental gradients. In turn, Hart et al. (2016) modelled the effects of intraspecific trait plasticity in homogeneous environments and found variation to increase dominance of superior competitors, to decrease niche differentiation and, in consequence, to reduce diversity. Dallas et al. (2021) reported similar effects in replicated *Tribolium* experiments. These ideas have gained support in outdoor studies on tropical tree plantations by Proß et al. (2021). However, field studies that link plasticity with diversity and environmental conditions are still lacking.

The variability in species traits is increasingly analysed with respect to allometric variance – mean relationships (VMR, e.g. Taylor 2019; Lagrue et al. 2015; Ulrich et al. 2021). Stochastic resampling theories predict that the variance  $\sigma^2$  should scale to the mean  $\mu$  by the power function

$$\sigma^2 = c \times \mu^z$$

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where  $c$  and  $z$  are the parameters (e.g. Keil et al. 2010; Kendal and Jørgensen 2011). Taylor's power law of population and community ecology is one example of this relationship (Taylor 1961; Taylor 2019). Poisson random variability is equivalent to a power function slope parameter  $z = 1$ , while Brownian motion processes (random walks) generate a slope of  $z = 2$ . Recently, Ulrich et al. (2021) reported the VMR of important woody plant functional traits to follow power laws with slopes  $z > 1$ .

Allometry might have consequences for community assembly. For example, competition theory predicts a negative correlation between resource use in important niche dimensions and community richness (Chesson 2000). However, if high trait variability promotes diversity (Proß et al. 2021; Dallas et al. 2021) these contrasting effects might affect community assembly, possibly masking single effects. Such contrasting impacts of mean trait expression and the respective variance have so far mainly been studied with respect to spatial aggregation of individuals (Yan et al. 2018) and resources (Fajardo and Siefert 2018). Aggregation, equivalent to a high variance in resource distribution, tends to increase local diversity (Hartley and Shorrocks 2002; but see Veech et al. 2003). To our knowledge, the impact of intraspecific trait variability on community assembly has not been studied so far.

Here, we try to fill these knowledge gaps and link the intraspecific variability of important functional traits in Polish mixed temperate forest understorey plants to small scale community assembly and functional diversity. We focus on the small balsam *Impatiens parviflora*, a dominant species in these forests (Ulrich et al. 2021). As *I. parviflora* is not only dominant but also one of the largest herbaceous species it locally accounts for more than half of the total understorey plant biomass (Ulrich et al. 2021). Therefore, we expected to see detectable effects of trait expression and trait variability of this species on the abundances, community composition, and species richness of other plants. Particularly, we hypothesise that 1) the variability in important functional traits of *I. parviflora* scales according to a power function, 2) this scaling affects community assembly, 3) higher trait variability decreases community diversity, and 4) trait variability is mainly determined by environmental variability. Importantly, we look at small scale community assembly within the interaction horizons of single *I. parviflora* ramets. At such spatial scales the impact of interspecific competition should be most detectable, while environmental filter effects should be comparatively small.

## Material And Methods

### Study sites and sampling

In June and July 2020 understorey plant samples were undertaken in 25 4 × 4 m<sup>2</sup> plots each at two semi-natural mixed temporal forest sites near Toruń (53.2°N, 18.5°E) in Northern Poland (cf. Ulrich et al. 2021 for detailed descriptions of the study sites). Plots within each site were selected for homogeneous soil and microclimate conditions. For the present study we randomly selected 41 subplots (1 m<sup>2</sup> each) from these plots and identified all understorey herbaceous species and woody plant saplings. For the study of intraspecific variability, we chose the dominant small balsam (*Impatiens parviflora*), which accounted for 1398 of all 1930 individual plant ramets (from 37 species) in these subplots. Other species were generally too rare within single subplots for a sufficiently precise analysis of individual trait variability. The complete set of raw data is contained in Appendix A and has been uploaded to figshare (to be uploaded after acceptance).

### Plant traits and soil characteristics

For each *I. pariflora* ramet we measured three plant traits (specific leaf area SLA, leaf dry weight LDW, and stem height SH). Additionally, we counted the total number of ramets NI and the number of flowers NF. For all other species we counted total abundances Nother and species richness Sother in each subplot. We determined five basic soil parameters using standard methods described in Ulrich et al. (2021): soil water (SWC), total organic carbon (TOC), nitrogen (N) content, the respective C / N ratio, and exchangeable basic cation ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ ,  $\text{Na}^+$ ) content from topsoil samples taken in the center of each plot. All trait and soil data are contained in Appendix A.

## Data analysis

For each subplot we calculated the arithmetic mean  $\mu$  and total trait expression  $\Sigma$  of the four *I. pariflora* traits measured, as well as the respective variances  $\sigma^2$ , and skewness  $\gamma$ . The skewness is often positively correlated with the variance and quantifies the importance of outliers, a neglected aspect in trait analyses. Trait variability  $\Delta V$  within each subplot was assessed from eq. 1 and the residuals of observed variance  $\sigma_o^2$  and the variance  $\sigma_p^2$  predicted by eq. 1 .

$$\Delta V = \sigma_o^2 - \sigma_p^2 = \sigma_o^2 - c\mu_p^z$$

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We compared  $\Delta V$  and  $\gamma$  for plots having <3 or  $\geq 3$  non-*I. pariflora* species and <10 or  $\geq 10$  non-*I. pariflora* ramets. We also used general linear modelling to link trait expression,  $\Delta V$  and  $\gamma$  to soil and community characteristics. Variables were Z-transformed prior to analysis. Errors always refer to standard errors.

We used principal components analysis (PCA) to reduce the dimensions of soil variables. The first two components (PC1, PC2) accounted for 53.2% and 44.0% of variance and loaded highest with SWC ( $r = -0.72$ ) and Ca ( $r = 0.70$ ), respectively. The correlation matrix for all variables used here is contained in Appendix B, Table S1. Bray-Curtis dissimilarity based PERMANOVA is a well-introduced method to assess changes in community composition across one or two categorical variables. Here, we used two way PERMANOVA to assess whether high or low variability in trait expression affects subplot species composition. For this task we used Z-transformed  $\Sigma$ ,  $\sigma^2$ ,  $\Delta V$ , and  $\gamma$ -values with codes 1 for positive and 2 for negative Z-values.

## Results

Average values of LDW, SH, and SLA were only marginally correlated with soil characteristics and community size (Table S2). SWC was positively correlated with  $N_I$ ,  $N_{\text{other}}$  and  $S_{\text{other}}$  and negatively with  $N_F$  (Table S2).  $N_I$  was significantly positively correlated with  $N_{\text{other}}$  explaining 26% of variance in  $N_{\text{other}}$  (Fig. 2a). In turn,  $N_I$  and  $S_{\text{other}}$  were not significantly related (Fig. 2b). Numbers  $N_{\text{other}}$  (Table 1) and also  $S_{\text{other}}$  (Table S3) were negatively linked to PC1, interpreted as soil water axis, and positively linked to PC2, the soil mineral axis (Table 1). Interestingly,  $N_{\text{other}}$  was significantly negatively correlated with  $N_F$  (Table

1). Variability in trait values as quantified by  $\Delta V$  and  $\gamma$  did not significantly depend on soil characteristics (Tables S4, S5). Soil variables explained less than 10% of variance in  $\Delta V$  and  $\gamma$  (Tables S4, S5).

Table 1

General linear modelling with abundance of non- *I. parviflora* ( $N_{\text{other}}$ ) species as response variable.

Given are  $\beta$ - and partial  $\eta^2$ -values, and model coefficients of determination  $r^2$ . Parametric significances: \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$ . N = 41.

Predictor	$N_{\text{other}}$							
	$\beta$	partial $\eta^2$	$\beta$	partial $\eta^2$	$\beta$	partial $\eta^2$	$\beta$	partial $\eta^2$
PC1	-0.22	0.05	-0.29*	0.11*	-0.37*	0.11*	-0.25	0.09
PC2	0.35*	0.14*	0.22	0.06	0.29	0.08	0.16	0.04
LDW	-0.20	0.04	-	-	-	-	-	-
$\Delta V$ LDW	0.03	<0.01	-	-	-	-	-	-
SH	-	-	-0.37*	0.15*	-	-	-	-
$\Delta V$ SH	-	-	0.13	0.02	-	-	-	-
SLA	-	-	-	-	0.18	0.03	-	-
$\Delta V$ SLA	-	-	-	-	0.06	<0.01	-	-
$N_F$	-	-	-	-	-	-	-0.51***	0.27***
$\Delta V$ $N_F$	-	-	-	-	-	-	0.06	<0.01
$r^2$		0.26*		0.30*		0.36*		0.44***

The variance – mean relationships of LDW, LH, and  $N_F$ , but not of SLA, closely followed power functions (eq. 1) with slope values  $z > 1.5$  (Fig. 3). Distributions of all four traits, particularly of LDW and  $N_F$ , were on average right skewed (LDW:  $y = 1.22 \pm 0.10$ ; SH:  $y = 0.19 \pm 0.08$ ; SLA:  $y = 0.67 \pm 0.37$ ;  $N_F$ :  $y = 0.80 \pm 0.09$ ).

Except for SLA, abundances of non- *I. parviflora* species significantly decreased within increasing variance in *I. parviflora* trait expression (Fig. 4). This was not the case with respect to non- *I. parviflora* species richness (Fig. S1), where richness and trait variance were not significantly correlated. However,  $\Delta V$  and  $\gamma$  differed between subplots of lower and higher species richness or abundance of non- *I. parviflora* species (Fig. 5). Higher  $\Delta V$  in LDW and  $N_F$  was associated with increased subplot richness and abundance (Fig. 5) although these patterns explained less than 10% of variance when accounting for soil covariates (Table 1). Two-way PERMANOVA detected at most marginal effects of *I. parviflora* trait variability on community composition (Table 2). The highest impact had the variance  $\sigma^2$  of SLA explaining approximately 7% of variance in community composition (Table 3).

Table 2  
Two way PERMANOVA (Bray-Curtis dissimilarity) to assess changes in plant community composition (excluding *I. parviflora*). N = 41.

Factor	LDW		SH		SLA		$N_F$	
	pseudo $r^2$	P						
$\Sigma$	0.05	0.04	0.04	0.13	0.02	0.52	0.05	0.08
$\sigma^2$	0.05	0.05	0.02	0.51	0.07	0.01	0.06	0.04
$\Sigma \times \sigma^2$	0.01	0.85	0.07	0.02	0.02	0.73	0.01	0.89
$\Delta V$	pseudo $r^2$	P						
	0.01	0.96	0.04	0.20	0.06	0.02	0.03	0.45
$\gamma$	0.03	0.44	0.04	0.11	0.04	0.10	0.03	0.34
$\Delta V \times \gamma$	0.02	0.65	0.03	0.29	0.02	0.65	0.04	0.23

## Discussion

Our results confirm the general tendency for power function VMRs of ecological variables (Fig. 2). In this respect, Taylor's power was originally formulated to describe the temporal dynamics of populations and spatial distributions of individuals (Taylor 1961; Taylor 2019). Recently, Lagrue et al. (2015) and Ulrich et al. (2021) extended the applicability of allometric VMR to spatial distributions of species traits. In this respect, it is worth to recall how power functions might appear. The easiest process involves linear proportional changes in the fractions of two variables, in this case an average value and the associated variance;  $\frac{d\sigma^2}{\sigma^2} = z \frac{d\mu}{\mu} \rightarrow \sigma^2 = c\mu^z$ . Given that traits values can vary equiprobably between fixed upper and lower limits, any increase in average trait will automatically result in a proportional increase in variance. Consequently, we argue that the appropriate null hypotheses of species trait variability is a power function VMR. In the case of linearly equiprobable probability of trait expression between the upper and lower boundaries, the VMR exponent will have a value of  $z = 2$  according to the equiprobable resampling model. This is exactly the pattern reported here with respect to LDW, SH, and  $N_F$  (Fig. 3), by this answering positively to our first starting question.

Lack of and also deviations from an allometric VMR, as calculated here by  $\Delta V$ , point to ecological processes causing different patterns of trait variability. Similar to Ulrich et al. (2021) we found SLA not to obey the allometric VMR (Fig. 3). SLA does not stem from a single measurement but is the ratio of leaf area and dry mass. If area ( $A$ ) and mass ( $M$ ) variances scale allometrically to their respective means with

$$\text{similar exponents } z, \text{ the quotient } \frac{\sigma_A^2}{\sigma_M^2} = \left( \frac{\mu_A}{\mu_M} \right)^z = (SLA)^z = \sigma_{SLA}^2 \approx \text{const. (2)}$$

in accordance with our finding. Compound traits are obviously not suited for the study of allometric variability and community assembly.

Negative local species co-occurrences have traditionally been interpreted as evidence for interspecific competition for limiting resources where a mass effect of one species (numbers of individuals) naturally reduces the numbers of other species (Chesson 2000). However, the ubiquity of allometric VMR offers the interpretation that it is not the mean number that is decisive but the variance in the occurrence of these numbers or, as in the present case, the variability in the expression of important functional traits that define niche dimensions. As this variability was directly negatively linked to the occurrences in the individuals (Fig. 4), the variability in trait expression among individuals translates into a spatial variability in trait expression. Trait variability as an agent in community assembly has only received minor interest (e.g. Jung et al. 2010; Violle et al. 2012; Westerband et al. 2021). For instance, Wakatsuki et al. (2021) showed how deer feeding induced intraspecific understorey plant trait variability determines plant community structure. Araújo et al. (2021) demonstrated how intraspecific leaf trait variability facilitates tropical tree diversity. Interestingly, Gianoli et al. (2021) linked phenotypic plasticity of forest plants to filter processes arguing that plasticity diminishes local filter effects allowing for additional species to enter local plant communities. Consequently and as an answer to our second starting question, we argue that an individual based study of local trait variability might return important insights into the composition and assembly of local communities.

Our third starting question asked whether higher trait variability decreases community diversity. In this respect, Hart et al. (2016) argued that higher trait variability should increase abundances of the dominant species. These authors analysed classical two species competitive models including intraspecific trait variation and found trait variation to decrease diversity by widening the niche space of the stronger competitor. However, whether such simple models also refer to the more complicated assembly dynamics of multi-species communities remains unclear. Indeed, neutral models (Hubbell 2005; Fridley et al. 2007) predict trait variation to increase local diversity. Moreover, models and empirical studies that include intransitive species competition also predict co-existence (Soliveres et al. 2015, Ulrich et al. 2017).

One mechanism generating competitive intransitivity might be intraspecific niche variability. Our results (Fig. 4) only partly corroborate the predictions of Hart et al. (2016) and a similar model of Dallas et al. (2021). We found indeed a negative correlation between trait variability of the dominant species and the abundances of all other species within each local community (Fig. 4) but these trends were not accompanied by a respective decrease in species richness as predicted by theory (Fig. S1). Trait variability was also not significantly related to community composition (Table 2). As both of our study forests are old-grown with comparatively low anthropogenic influence successional dynamics should not influence our results. Further, abundances of *I. parviflora* and the abundances and species richness of all other species were positively correlated (Fig. 2). Therefore, we conclude that the potential negative impact of lower abundances due to a high trait variability of the dominant species does not significantly impact local richness. Apparently, counterbalancing mechanisms exist that stabilize diversity. One such mechanism might be the constant colonization input from the surrounding forest plants making local

communities dynamically stable despite of marked dominance orders. We have to remember that our plots were artificial units in a continuous matrix of plants.

Interestingly, deviations in abundance and species richness from the null expectation were in contrast to the trait variance – abundance pattern showing that deviations from a statistical standard (Fig. 4) might contain additional information not obvious from the patterns in raw data (Fig. 3). This fact is well known in community assembly theory (Ulrich and Gotelli 2013). Higher *I. parviflora* trait divergence  $\Delta V$  was associated with higher local abundance and species richness (Fig. 4). Again, this finding contradicts the models of Hart et al. (2016) and Dallas et al. (2021). Importantly, higher diversity and abundances were linked to higher skewness of the trait distributions of LDW and N<sub>F</sub>. To our knowledge the influence of trait skewness has so far not been studied with respect to community assembly. Our results call for new theoretical and empirical approaches to the dependence of local community pattern on trait variability. Such approaches should include the study of traits of all species and not only of dominant ones.

With regard to our fourth starting question we did not observe that trait expression and the respective variances were significantly determined by averaged values of soil factors (Figs. S2, S4). In our study sites higher water content correlated negatively and higher mineral content positively with abundance and species richness (Tables 1 and S3). Therefore, we expected to see respective influences of soil characteristics on trait expression as soil nutrient availability is known to influence trait expression and spatial variability either by plant plasticity (e.g. Borowy and Swan 2020) or genetic differentiation (e.g. Born and Michalski 2019). Apparently, our study plots located in two forests were environmentally too homogeneous to reveal marked influences of soil factors. Consequently, we argue that habitat filter effects should not significantly influence the above results on trait variability.

Our study has two major shortcomings that do not allow for a more functional interpretation of our results. First, due to the fact that we studied only one vegetation season, temporal species turnover of the subdominant species was not assessed. Even in seemingly stable semi-natural old-grown forest temporal turnover might be an important factor in small scale community assembly, thus masking the effects of competitive superiority and spatial distributions (Ulanova 2000). Second, due to limitations in manpower, our studies was done at a one m<sup>2</sup> resolution (still including 1398 single ramets to be analysed morphometrically). A higher resolution and a correspondingly increased sample size might have revealed species- and ramete- pair trait relationships. Such an approach should directly reveal competitive interactions and, applied to the whole community, should allow for the construction of species  $\times$  species competitive interaction matrices, necessary to reveal multispecies competitive hierarchies and loops (Soliveres et al. 2015). We call for respective individual based studies of local plant trait and species co-occurrences (cf. Ulrich et al. 2021).

## Declarations

### Author contribution

WU devised the study, analysed the data and wrote the draft text. PO did the field and laboratory work, the image processing, and finalised text. PS analysed the soil data. RP and MK provided plant trait data and conceptual input. All authors contributed to the final text.

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** All authors read the final manuscript version and agreed to publish the data contained in this study.

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**Availability of data** All raw data contained in this study are contained in the supplementary file Appendix A and B.

**Code availability** Not applicable.

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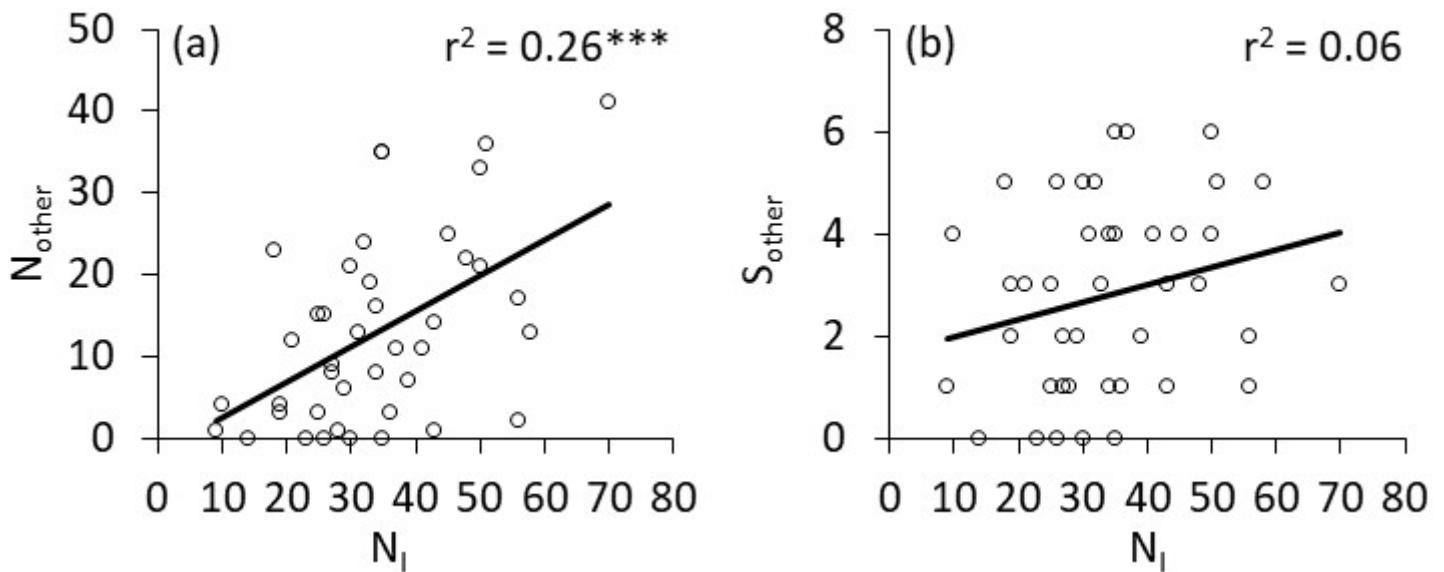
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## Figures



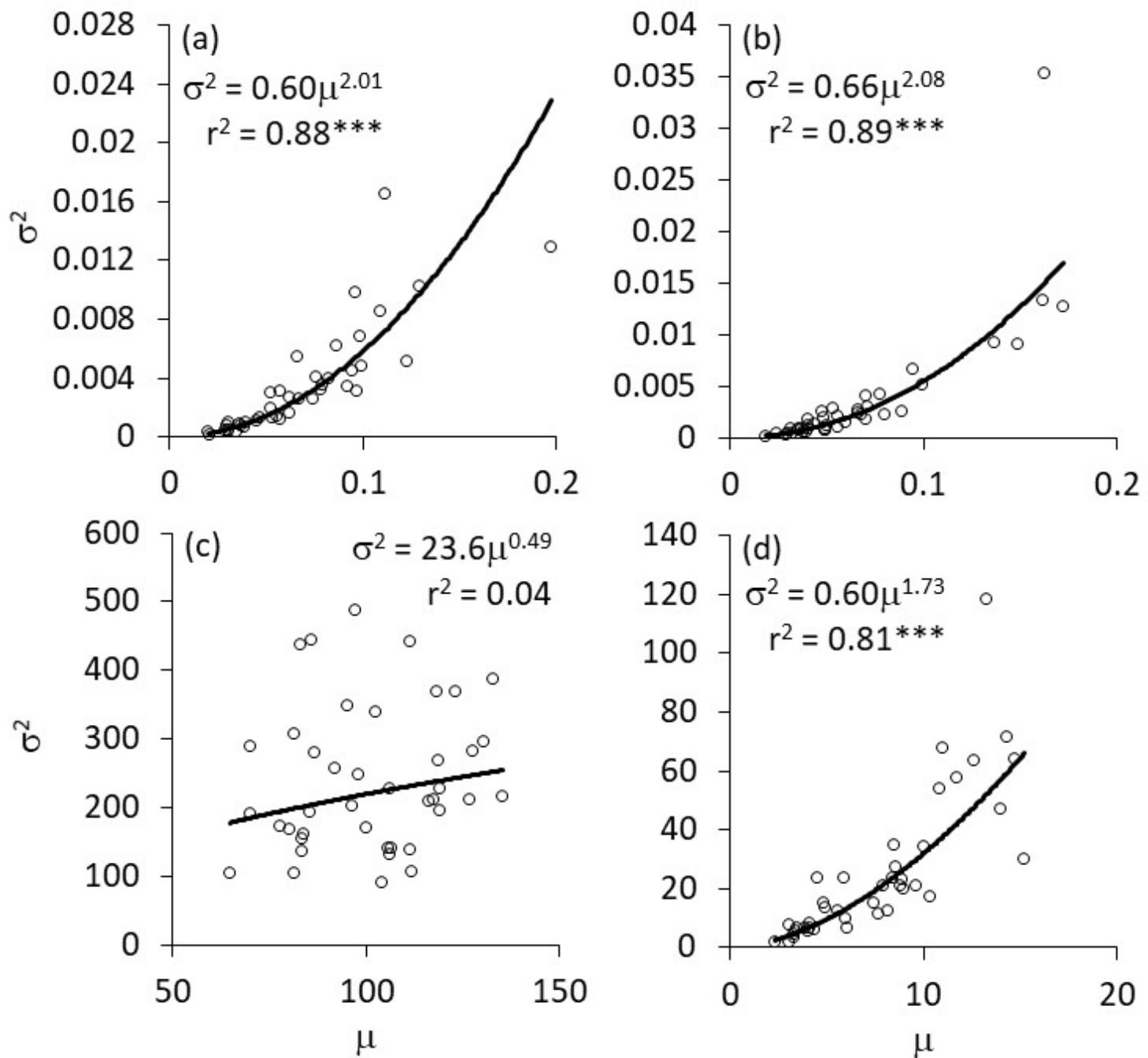
**Figure 1**

typical 4×4 m<sup>2</sup> plot at Piwnicki forest reveals the dominance of *Impatiens parviflora*.



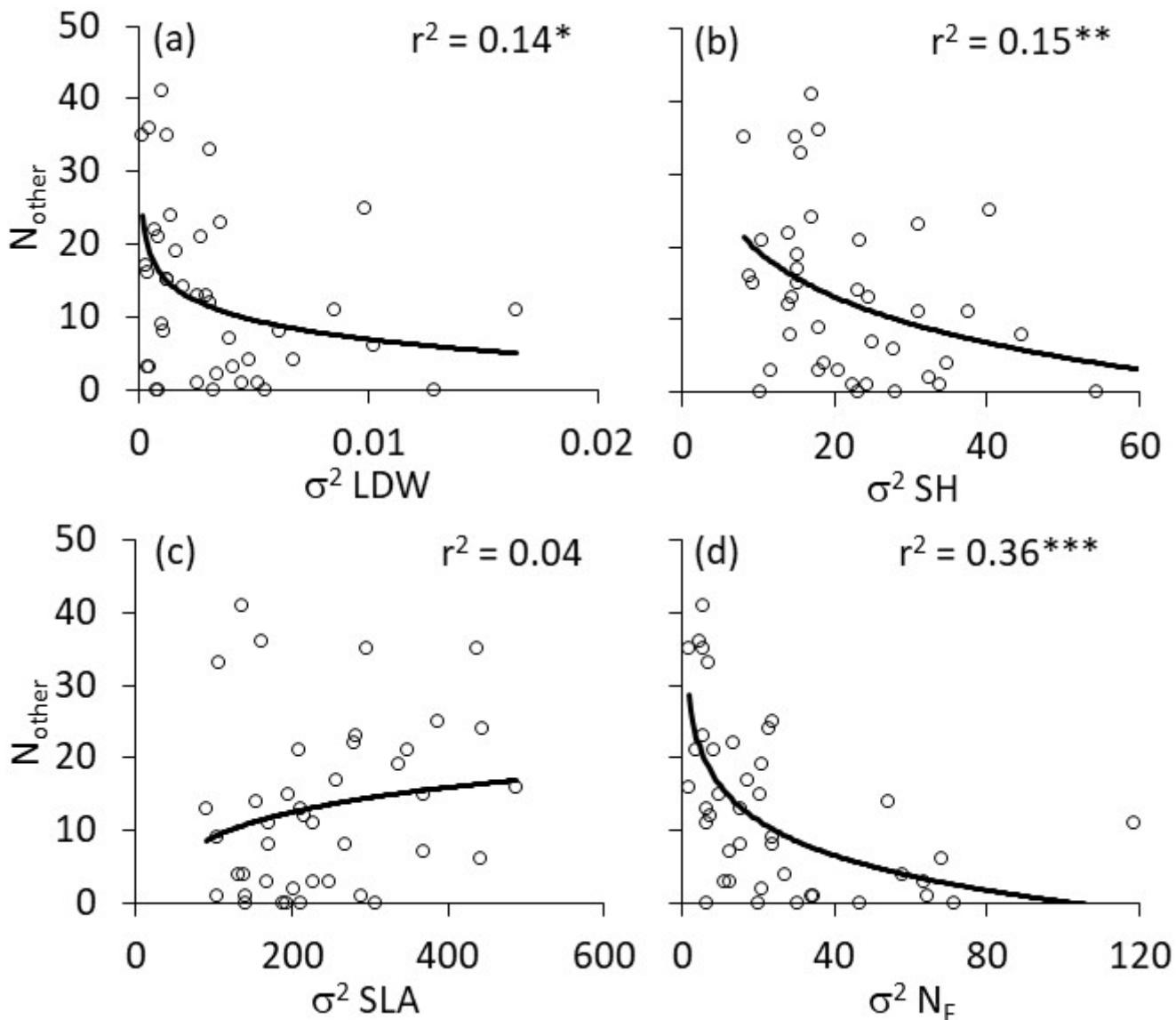
**Figure 2**

Relationships between numbers of *Impatiens parviflora* ( $N_I$ ) per study subplot and total numbers of other species (a:  $N_{\text{other}}$ ) and richness of other species (b:  $S_{\text{other}}$ ). Given are ordinary linear least squares regressions (\*\*\*:  $P < 0.001$ ).



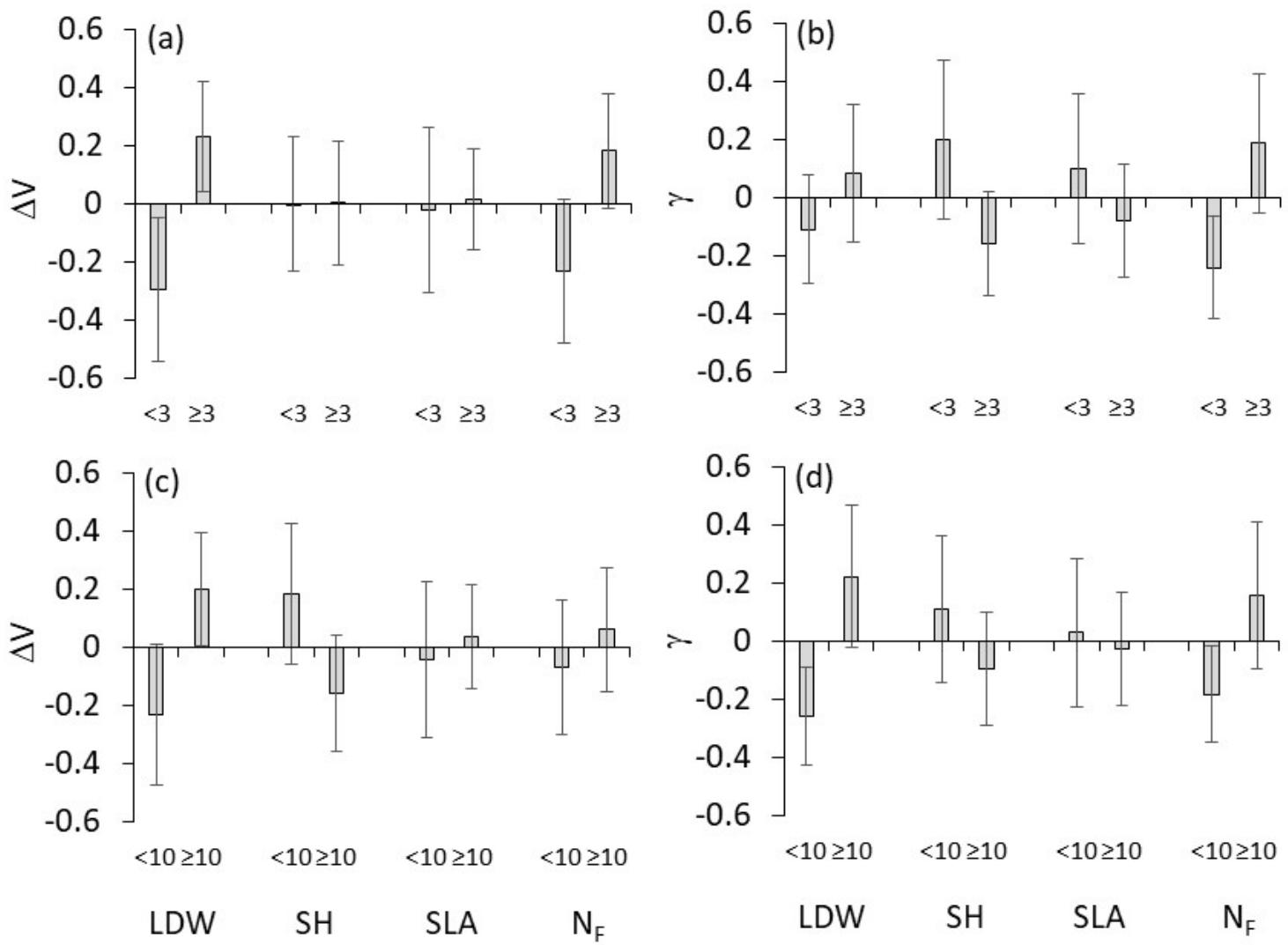
**Figure 3**

The variance ( $\sigma^2$ ) – mean ( $\mu$ ) relationships for LDW (a), SH (b), SLA (c), and NF (d).



**Figure 4**

Relationships between the abundances of non-*I. parviflora* species ( $N_{\text{other}}$ ) and the variances of a) leaf dry weight (LDW), b) stem height (SH), c) specific leaf area (SLA), and d) number of flowers ( $N_F$ ) of *I. parviflora* rametes within 41 subplots. Parametric significances of logarithmic OLS regressions: \*:  $P < 0.05$ , \*\*:  $P < 0.01$ , \*\*\*:  $P < 0.001$ .



**Figure 5**

Differences in average  $\Delta V$  (a, c) and  $\gamma$  (b, d) between subplots  $<3$  or  $\geq 3$  non *I. parviflora* species (a, b) and  $<10$  or  $\geq 10$  rametes of non *I. parviflora* species (c, d). Error bars denote standard errors.

## Supplementary Files

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