1 Original Article

2 Decomposing intraspecific phenotypic variation: implications for species and functional

3 diversity

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20 Running Title: Decomposing intraspecific variation

21

1 **Abstract**

2 *Background and Aims.* Researchers have a long history of seeking an explanation for and

3 understanding of diversity patterns. High-dimensional trait-based trade-offs have been

4 hypothesized as being important for maintaining species and functional diversity. These

5 relationships have primarily been investigated at the community-level rather than within species,

6 despite the importance of intraspecific variation to species and functional diversity maintenance.

7 The goal of this research is to determine if trait combinations are present within species and the

8 impacts of this on species and functional diversity in a tropical forest seedling community in

9 China. We ask 1) do the trait combinations found across species, at the community-level, also

10 exist within species?; 2) how consistent or inconsistent are trait combinations across species?;

11 and 3) how do findings align with species co-occurrence patterns?

12 *Methods.* We model species-specific growth with individual-level trait measurements,

13 environmental data, and their interactions, allowing for the identification of intraspecific trait

14 combinations and quantification of the contribution of each model variable to growth.

15 *Key Results.* We find that two of three species have intraspecific trait combinations. Specifically,

16 we find that individuals within these species share a trait combination, but how they combine the

17 traits differs depending on the type and level of soil nutrients. Furthermore, we find that

18 similarity among species in trait combinations and variables that contribute most positively to

19 growth may lead to negative spatial co-occurrence patterns of species.

20 *Conclusions.* Overall, we find that species have multiple traits or interactions between traits and

21 the environment driving their species-specific strategies for growth success. These results

22 highlight how individuals within species are highly variable, with phenotypically different

1   individuals having similar growth performance, and suggest how high species and functional

2   diversity can be maintained in communities.

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4   Key Words: diversity, functional traits, growth, intraspecific variation, seedlings, trait

5   combinations, tropical forest

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1 **Introduction**

2 Ecologists have long investigated, and struggled to explain, the mechanisms that maintain

3 species diversity (Hutchinson, 1961; Clark, 2010). Diversity patterns are driven by differential

4 demographic outcomes, which arise from how phenotypes interact with the environment

5 (Ackerly, 2003, HilleRisLambers et al., 2012). Relationships between phenotypes, the

6 environment, and demographic outcomes are complex, but high-dimensional trait-based trade-

7 offs have been hypothesized as being important for maintaining species and functional diversity

8 in communities (Clark et al., 2010, Adler et al., 2013, Kraft et al., 2015; D'Andrea and Ostling,

9 2016). While these relationships have been investigated at the community level, the presence of

10 these complex relationships within species has gone largely unconsidered in trait-based

11 community ecology, despite the known importance of intraspecific variation for generating and

12 maintaining species and functional diversity (Hart et al., 2016; Turcotte and Levin, 2016).

13   One way ecologists have examined the relationships between phenotypes, the

14 environment, and demographic rates is by investigating the presence of different trait

15 combinations. (Marks and Lechowicz, 2006; Adler et al., 2014; Laughlin and Messier, 2015;

16 Dwyer and Laughlin, 2017; Laughlin et al., 2018). Often these studies seek to link variation and

17 trade-offs in functional traits to variation in the environment or demographic rates (Laughlin and

18 Messier, 2015; Laughlin et al., 2018; Dias et al., 2019; Li et al. 2021). Previous research has

19 found evidence of demographic success linked to multiple trait combinations at the community-

20 level both within and across environmental gradients (Laughlin et al., 2018; Dias et al., 2019;

21 Worthy et al., 2020; Li et al., 2021).

22   A major theme from previous work is that although there is evidence of multiple trait

23 combinations leading to demographic success, the number of combinations is relatively small

1 compared to the number of species in the study systems (Dias et al., 2019; Pistón et al., 2019;

2 Worthy et al., 2020; Li et al., 2021). For example, Worthy et al. (2020) found evidence of only

3 eight different trait combinations in a community composed of 122 species. To reconcile the low

4 number of trait combinations found in communities with high levels of species diversity, one

5 may assume that multiple species must have the same combination of traits leading to

6 demographic success.

7 Based on the assumption that multiple species have the same trait combination, initial

8 hypotheses can be made about how high species and functional diversity can be maintained in

9 communities with so few ways for species to achieve demographic success. One hypothesis

10 could be that some species have highly variable traits allowing individuals within a species to

11 have different trait combinations that overlap with those of other species, limiting the total

12 number of combinations found in a community. The alternative to this hypothesis would be that

13 each species, in fact, does have a unique trait combination that is consistent among individuals.

14 This would mean that each species is a specialist, each with their own way of achieving

15 demographic success (MacArthur and Levins, 1967; Tilman, 1982). However, as highlighted

16 above, prior research has shown that this hypothesis is unlikely to be supported (Laughlin et al.,

17 2018; Pistón et al., 2019; Worthy et al., 2020; Li et al., 2021). What is more likely is that

18 multiple species share the same trait combination that confers similar demographic outcomes.

19 The maintenance of multiple species in a community having the same trait combination

20 would likely only be possible if species are temporally or spatially segregating the environment.

21 Species could benefit from temporal segregation through the storage effect, where species with

22 the same trait combination are favored at different time periods (Chesson and Warner, 1981;

23 Chesson, 2000; Adler et al., 2013). Species could also spatially segregate to reduce competition

1   when they have the same trait combination (Chesson, 2000; Wright, 2002), which may be

2   evident in co-occurrence patterns of species. Both of these scenarios would appear as a low

3   number of trait combinations at the community-level, even though species and functional

4   diversity could be high. Of course, there could be a combination of all of these possibilities at

5   work.

6   The goal of the present research was to determine if trait combinations are present within

7   species and the impacts of this on species and functional diversity in a tropical forest seedling

8   community. We asked three questions, 1) do trait combinations found across species, at the

9   community-level, also exist within species?; 2) how consistent or inconsistent are trait

10   combinations across species?; and 3) how do findings align with species co-occurrence patterns?

11

12   **Material and Methods**

13   *Study Site*: The data set used in this study comes from a tropical forest seedling community in

14   Xishuangbanna, in the Yunnan province of China (101°34´E, 21°36´N). The climate for this area

15   is monsoonal with two seasons, the dry season that spans November to April and the wet season

16   that spans May to October (Cao et al., 2008). The mean annual temperature is 21.8 °C and mean

17   annual precipitation is 1,493 mm, with 85% of the precipitation occurring during the wet season

18   (Cao et al., 2008).

19

20   *Seedling Plot Establishment and Monitoring*: A total of 218 m^2 seedling plots were installed

21   across an approximate area of 2-ha where all seedlings with a height of less than or equal to 50

22   cm were tagged and identified. Height of these seedlings was taken during the installation of the

1   plots and at the end of a yearlong census from 2013-2014. Surviving seedlings were then

2   harvested for functional trait quantification.

3

4   *Species Data Set*: Most species in this community were rare, with few common species. Since

5   this study focuses on variation within species, many species were eliminated from analyses due

6   to lack of abundance. There were 122 species total among the plots, but this study includes the

7   three species with at least 100 individuals, each from a different genus and family

8   (Supplementary data Table S1).

9

10   *Functional Traits*: Two functional trait measurements were taken on each harvested seedling.

11   One organ-level trait, leaf mass per unit area (LMA), and one biomass allocation trait, root mass

12   fraction (RMF; total root mass divided by whole plant mass). LMA was measured on one to

13   three leaves for each individual. RMF was measured according to (Poorter et al. 2012) and

14   previously reported in Umaña et al. (2015). Leaves and roots were manually separated in the lab

15   and dried in the oven for 72 h at 70 °C. Trait variables were natural log-transformed and scaled

16   to a mean of zero for each species separately prior to analyses (Supplementary data Table S1).

17   These two traits (LMA and RMF) were specifically chosen for measurement as they

18   represent major allocation tradeoffs at both the organ and whole plant levels that should impact

19   growth success. LMA represents the leaf economics spectrum (Reich et al., 1997, Wright et al.,

20   2004) where species with higher LMA have lower mass-based photosynthetic rates, but longer

21   leaf lifespans and species with lower LMA have higher mass-based photosynthetic rates, but

22   shorter leaf life spans. RMF is often measured to quantify allocation to non-photosynthetic

23   tissues.

1

2   *Quantifying Growth Rates*: To determine the relative growth rate (RGR) of each individual, the

3   change in log-transformed height was calculated as:

4    $$\text{RGR} = (\log(M_{t+\Delta t}) - \log(M_t))/\Delta t$$

5   The variable M_t is the height at successive time steps t (Hoffmann and Poorter, 2002). A

6   value of 1 was added to all observed RGR values and the data were then natural log-transformed

7   and scaled to a mean of 0 to approximate normality for each species separately. Relative growth

8   rate served as the demographic rate of interest in this study.

9

10   *Environmental Variables*: Light availability and soil nutrients were measured once for each plot

11   (Supplementary data Table S2). Light availability was measured as the percent canopy openness

12   determined using photographs taken with a Nikon FC-E8 lens and a Nikon Coolpix 4500 camera

13   one meter above the ground over each plot before sunrise with cloudy conditions. Images were

14   analyzed using Gap Light Analyser software (http://www.caryinstitute.org/science-program/our-

15   scientists/dr-charles-d-canham/gap-light-analyzer-gla). To measure soil nutrient levels, 50 g of

16   the topsoil (0-10 cm in depth) was collected from each corner of each plot. Samples were air

17   dried and sifted before analyses. Cation availability was determined using the Mehlich III

18   extraction method and atomic emission inductively coupled plasma spectrometry (AE-ICP).

19   Total nitrogen and carbon content were determined by total combustion using an auto-analyzer

20   and pH measured with a pH meter. All soil analyses were conducted at the Biogeochemical

21   Laboratory at Xishuangbanna Tropical Botanical Garden.

22   The environmental variables were natural log-transformed and scaled to a mean of zero

23   before analyses. Soil nutrients were condensed into principal components and the first two

8

1   orthogonal axes were used in analyses with 39% of the variation explained by the first axis and

2   21% of the variation explained by the second axis (Supplementary data Table S3). PC1 scores

3   were negatively associated with K, Mg and Zn and PC2 scores were negatively associated with

4   Ca and P (Supplementary data Fig. S1).

5

6   *Linear Mixed-Effects Model Description*: To determine species' relationships between traits, the

7   environment, and relative growth rate, we built linear mixed effects models using a Bayesian

8   approach for each species separately. Variables were chosen for inclusion in the model based on

9   prior evidence of their significant effects on growth performance (Baraloto et al., 2006; Poorter

10 et al., 2012; Reich, 2014; Umaña et al., 2018; Worthy et al., 2020). For each species' model,

11 RGR followed a log-normal distribution:

12 $$\mathrm{logRGR_i} \sim N(z_i, \sigma_z),$$

13 where z_i was the relative growth rate of each individual and σ_z was the variance. The general

14 formula of the model was:

15 $z_i = \alpha_p + \beta_1 \mathrm{LMA} + \beta_2 \mathrm{RMF} + \beta_3 \mathrm{Initial\ Size} + \beta_4 \mathrm{Light} + \beta_5 \mathrm{Soil1} + \beta_6 \mathrm{Soil2} + \beta_7 \mathrm{LMA} \times \mathrm{RMF}$

16 $\qquad\qquad + \beta_8 \mathrm{LMA} \times \mathrm{Light} + \beta_9 \mathrm{LMA} \times \mathrm{Soil1} + \beta_{10} \mathrm{LMA} \times \mathrm{Soil2} + \beta_{11} \mathrm{RMF} \times \mathrm{Light}$

17 $\qquad\qquad + \beta_{12} \mathrm{RMF} \times \mathrm{Soil1} + \beta_{13} \mathrm{RMF} \times \mathrm{Soil2} + \beta_{14} \mathrm{LMA} \times \mathrm{RMF} \times \mathrm{Light}$

18 $\qquad\qquad + \beta_{15} \mathrm{LMA} \times \mathrm{RMF} \times \mathrm{Soil1} + \beta_{16} \mathrm{LMA} \times \mathrm{RMF} \times \mathrm{Soil2},$

19 where z_i was the relative growth rate of each individual and α_p was a random effect for plot.

20 The plot random effect was given a diffuse normal prior for mean and a diffuse half-

21 Cauchy prior for variance, which is useful because it is a thick-tailed probability distribution that

22 is weakly regularizing (McElreath, 2016). All other variables were given diffuse normal priors.

23 All models were fit using Hamiltonian Monte Carlo sampling implemented in Stan (Stan

1   Development Team, 2020) interfaced with R programming language (R Development Core

2   Team, 2016) using the *rethinking* (McElreath, 2016) and *rstan* (Stan Development Team, 2020)

3   packages. We ran four independent chains with random initial values for 50,000 iterations and a

4   warm-up period of 5,000 iterations. Parameter estimates and 95% credible intervals were

5   obtained from the posterior distributions. Convergence of the chains along with each variable in

6   the model was assessed visually and using the Gelman-Rubin convergence diagnostic with a

7   cutoff value of 1.1 (Gelman and Rubin, 1992). A parameter was considered significant if its 95%

8   credible intervals did not overlap zero.

9

10   *Assessing Intraspecific Trait Combinations*: To determine the presence of trait combinations

11   within a species, two conditions had to be supported. First, the two-way interaction term between

12   LMA and RMF or any three-way interaction term, between the two traits and an environmental

13   variable, in the model had to be significant with 95% credible intervals around the parameter

14   estimate not overlapping zero. Second, the first partial derivative of the fitted model was

15   calculated to determine if the relationship between a trait and RGR switches signs across the

16   range of the other trait and/or environmental variable in the interaction (Laughlin et al., 2018;

17   Worthy et al., 2020).

18

19   *Quantifying Contribution of Variables to RGR*: We determined the contribution of each model

20   variable to RGR for each species by multiplying the partial regression coefficient, separately, by

21   the mean, minimum, and maximum observed trait and/or environmental variable following

22   Arnold (1983). This allowed us to determine for each species which model variable contributed

23   most positively to RGR and more specifically, the importance of trait combinations and their

1   interactions with the environment to RGR. The two principal component axes of the soil

2   variables included negative values so the exponentials of these values were used to eliminate the

3   negative values so that the contribution of these variables could be determined.

4

5   *Co-Occurrence Patterns*: Co-occurrence patterns of the species were determined using the

6   *cooccur* package (Griffith et al., 2016) in R based on the presence or absence of species across

7   the seedling plots. This function calculated the observed and expected frequencies of co-

8   occurrence between each pair of species, with the expected frequency based on the distribution

9   of each species being random and independent of the other species (Veech, 2013). The function

10   returned the probability of co-occurrence for all pairs of species along with pairs that have a

11   higher or lower value of co-occurrence than could have been obtained by chance.

12

13   **Results**

14   *Assessing Intraspecific Trait Combinations*

15   Each species' model was assessed for the presence of intraspecific trait combinations

16   (Supplementary data Table S4). Two of the three species showed evidence of trait combinations

17   with significant interactions found between the two traits (LMA and RMF) and between the two

18   traits and an environmental variable (Fig. 1). *Pseuduvaria indochinensis* (Annonaceae) did not

19   show evidence of trait combinations but did have two significant two-way interactions between

20   LMA and soil component 1 and the between RMF and light (Supplementary data Fig. S2).

21   *Parashorea chinensis* (Dipterocarpaceae) and *Pittosporopsis kerrii* (Icacinaceae) both showed

22   evidence of trait combinations each having a significant two-way interaction between LMA and

23   RMF (Fig. 2). For both species, RGR was higher when individuals had high LMA and low RMF

1   or when individuals had low LMA and high RMF (Fig. 2). A significant three-way interaction

2   was also found between the two traits and a component of soil nutrients in models of both of

3   these species. *P. chinensis* had a significant three-way interaction between LMA, RMF, and soil

4   component 2 (Fig. 3A). At the poor nutrient end of the soil nutrient gradient, individuals had

5   higher RGR when they combined low LMA with low RMF (Fig 3A). At the high nutrient end of

6   the soil variable, there were two peaks in RGR, one for individuals with high LMA and low

7   RMF and one for individuals with low LMA and high RMF (Fig 3A). *P. kerrii* had a significant

8   three-way interaction between LMA, RMF and soil component 1 (Fig. 3B). At the low nutrient

9   end of the soil gradient, individuals had higher RGR when they combined high LMA with high

10 RMF or low LMA with low RMF (Fig. 3B). At the opposite end of the soil gradient with high

11 nutrients, there were also two peaks in RGR, one for individuals with high LMA and low RMF

12 and one for individuals with low LMA and high RMF (Fig. 3B).

13

14 *Quantifying Contribution of Variables to RGR*:

15 The contribution of each model variable to RGR of each species was calculated at the mean,

16 minimum, and maximum observed values of each variable (Supplementary data Table S5). Of

17 the two traits in the models, LMA had a larger, direct contribution to RGR than RMF for all

18 species when not considering how the traits are influenced by environmental variables or each

19 other (Supplementary data Table S5). For two species, minimum LMA contributed most where

20 for *P. kerrii* maximum LMA contributed most to RGR (Supplementary data Table S5). For the

21 environmental variables, maximum observed light was the largest contributor to RGR for all

22 species (Supplementary data Table S5). Despite finding evidence of significant trait

23 combinations (Fig. 2) and that these combinations interact with soil nutrients (Fig. 3) for *P.*

1 *chinensis* and *P. kerrii*, these variables did not contribute most to RGR in these species. The

2 overall largest, positive contributor to RGR for these two species was the interaction between

3 maximum RMF and maximum soil component 2, high Ca and P in the soil (Supplementary data

4 Table S5). For *P. indochinensis*, maximum light was the largest contributing variable to RGR

5 (Supplementary data Table S5).

6

7 *Comparisons and Drivers of Species Trait Combinations*

8 One species in this study, *P. indochinensis,* did not show evidence of intraspecific trait

9 combinations. However, significant interactions were found for this species between singular

10 traits and environmental variables (Supplementary data Fig. S2). The two other species in this

11 study did show evidence of intraspecific trait combinations (Figs. 1-3). *P. kerrii* and *P. chinensis*

12 share one interaction term with evidence of multiple intraspecific trait combinations, LMA ×

13 RMF (Fig. 1-2). However, how individuals within these species combine these traits to achieve

14 higher RGR differs based on the type and level (low versus high) of nutrients in the soil (Fig. 3).

15 Interestingly, all three species significantly, negatively co-occur on the landscape

16 (Supplementary data Table S6), suggestive of species spatially segregating due to similarity in

17 trait combinations used to acquire resources.

18   While there was variation among species in the presence and type of trait combinations,

19 all species were similar in what variables contributed most to increased RGR (Supplementary

20 data Table S5). LMA dominated as a singular trait, but RMF was more common as part of

21 interaction terms for the largest overall contributing variable to increased RGR (Supplementary

22 data Table S5). All three species had the same environmental variable with the highest

23 contribution, maximum light, and two of the species had the same variable with the largest

13

1 overall contribution to RGR, maximum RMF interacting with maximum soil component 2

2 (Supplementary data Table S5). Similarity between all species for which variables contributed

3 the most to increased RGR could suggest an underlying best strategy for growth in this

4 community, but species capitalize on differentiation along other axes and/or use intraspecific

5 trait combinations to acquire resources for growth.

6

7 **Discussion**

8 In this study, we have shown that two of the three most abundant seedling species in a tropical

9 forest community have intraspecific trait combinations that, along with environmental variables,

10 contribute to both similarities and differences in how these species achieve growth success.

11 Below we discuss how variability in the presence, type, and importance of trait combinations

12 among species maintains both species and functional diversity in this community.

13 Two of the three species in this study showed evidence of intraspecific trait

14 combinations. Specifically, individuals within a species had trait × trait, and/or trait × trait ×

15 environment combinations that led to higher RGR (Fig. 1-3). Individuals within both *P.*

16 *chinensis* and *P. kerrii* combined LMA and RMF in the same two ways to achieve higher RGR

17 (Fig. 2). These findings support our hypothesis that species may have the same intraspecific trait

18 combination. We also found support for these species spatially segregating the environment, with

19 all species negatively co-occurring with the other species in the study (Supplementary data Table

20 S6). In addition to similar intraspecific trait combinations, all species in the study were similar in

21 what variables contributed most to increased RGR (Supplementary data Table S5). This could

22 suggest an underlying best strategy for growth in this community which species deviate from to

23 acquire limiting resources and decrease interspecific competition.

14

1   One way species may differentiate their strategies for growth in this community is by

2   altering how they combine traits along soil nutrient gradients. Interestingly, the trait

3   combinations of the two species combined in different ways while significantly interacting with

4   different soil nutrients (Fig. 3). This allows individuals within these species to change or

5   combine resource acquisition strategies (acquisitive and conservative) within and among

6   environments along soil nutrient gradients to achieve growth success (Fig. 3). The ability of

7   these species to alter how traits combine depending on the soil nutrient type and level supports

8   the hypothesis that some species have highly variable traits with individuals within a species

9   having different trait combinations that may overlap with other species. These results offer an

10   explanation as to how communities can have a low number of trait combinations, but high

11   species and functional diversity. Previous studies have suggested that high trait variability of

12   species could allow them to maintain dominance in communities which seems plausible here as

13   these species are some of the most abundant in this community (Richards et al., 2006; Hart et al.,

14   2016; Pérez-Ramos et al., 2019). However, we note that this study includes only three species

15   that are the most abundant in the seedling community and that we did not investigate moderately

16   abundant or rare species due to sample size issues. Importantly, however, our results highlight

17   that individuals within species are highly variable, with very phenotypically different individuals

18   having similar growth performance, suggesting that using species mean traits to estimate

19   individual growth or species mean growth may have critical conceptual and empirical

20   consequences (Yang et al., 2018; Swenson et al., 2020; Yang et al., 2020).

21   The species in this study showed evidence of species-specific strategies for growth across

22   multiple axes of trait and environmental variation. Commonly, we found that interactions

23   between traits and the environment contributed most to species' RGR, such that similarity in

15

1   how species' acquire resources for growth may depend on which end of the environmental

2   gradient the species is located in the community. A major takeaway from previous work was the

3   suggestion that there are only a few dimensions along which species compete where they can

4   partition resources and decrease interspecific competition (Clark et al., 2004; Condit et al., 2006;

5   Clark et al., 2007; Mohan et al., 2007; Clark, 2010). This dynamic has been discussed previously

6   as the paradox of low diversity where models tend to find low levels of species diversity, which

7   do not align with observed levels, and are unable to explain how so many species can inhabit

8   communities (Hutchinson, 1961; Clark, 2010). Our findings and others (D'Andrea et al., 2018),

9   however, highlight the large amount and multi-dimensional nature of species differences in how

10   they combine traits and alter traits along environmental gradients to acquire resources for growth

11   and suggest how high species and functional diversity can be maintained in communities.

12   Overall, our results suggest that these common species are assembled in this seedling

13   community via resource acquisition for growth along multiple as well as high-dimensional axes

14   of trait and environmental variation. Our findings stress that individuals within species are able

15   to exploit this multidimensionality in different ways, which would have gone unobserved in

16   species-level analyses (Clark, 2010). While observational, this study considers multiple

17   environmental variables, common functional traits, and their interactions to capture a broad

18   range of ecological dimensions used to distinguish how species acquire resources for growth and

19   understand how similarities and differences in resource acquisition strategies maintain species

20   and functional diversity. This study capitalizes on a central tenet of trait-based ecology,

21   differential demography can be attributed to phenotypic variation which should scale up to

22   explain emergent patterns in communities (McGill et al., 2006; Yang et al., 2020).

23

1   **Supplementary Information**

2   Table S1: Minimum and maximum observed values of each functional trait and relative growth

3   rate (RGR) of each species in the study, along with total number of individuals per species (n).

4   Table S2: Soil nutrient concentration and percent of light availability ranges for all 218 seedling

5   plots. Table S3: Principal component analysis loadings of the soil variables. Table S4: Mean

6   standardized coefficients for each of the three species in the study. Table S5: The contribution of

7   each model variable to RGR. Table S6: Results of co-occurrence patterns of the species. Figure

8   S1: Principal components analysis of the soil properties. Figure S2: *P. indochinensis* (PSEUIN,

9   373 individuals) had two significant two-way interactions.

10

3

4   **Open Data**

5   Data and code for the analyses in this manuscript are currently available on GitHub at

6   https://github.com/sjworthy/Intraspecific.Designs. A Zenodo DOI will be obtained for the

7   GitHub material upon manuscript acceptance.

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Literature Cited

Ackerly DD. 2003. Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Sciences* 164: S165-S184.

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB. 2013. Trait-based tests of coexistence mechanism. *Ecology Letters* 16: 1294-1306.

Arnold SJ. 1983. Morphology, performance and fitness. *American Zoologist* 23: 347-361.

Baraloto C, Bonal D, Goldberg DE. 2006. Differential seedling growth response to soil resource availability among nine neotropical tree species. *Journal of Tropical Ecology* 22: 487-497.

Cao M, Zhu H, Wang H, et al. 2008. *Xishuangbanna Tropical Seasonal Rainforest Dynamics Plot: Tree Distribution Maps, Diameter Tables and Species Documentation*. Kunming: Yunnan Science and Technology Press.

Chesson P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343-366.

Chesson PL, Warner RR. 1981. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist* 117: 923-943.

Clark JS. 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327: 1129-1132.

Clark JS, LaDeau S, Ibanez I. 2004. Fecundity of trees and the colonization-competition hypothesis. *Ecological Monographs* 74: 415-442.

Clark JS, Dietze M., Chakraborty S., et al. 2007. Resolving the biodiversity paradox. *Ecology Letters* 10: 647-662.

Clark JS, Bell D, Chu C, et al. 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs* 80: 569-608.

19

1 Condit R, Ashton P, Bunyavejcheqin S, et al. 2006. The importance of demographic niches to

2   tree diversity. *Science* 313: 98-101.

3 D'Andrea R, Ostling A, 2016. Challenges in linking trait patterns to niche differentiation. *Oikos*

4   125: 139-1385.

5 D'Andrea R, Ostling A, O'Dwyer JP. 2018. Translucent windows: how uncertainty in

6   competitive interactions impacts detection of community pattern. *Ecology Letters* 21: 826-

7   835.

8 Dias ATC, Rosado BHP, de Bello F, Pistón N, de Mattos EA. 2019. Alternative plant designs:

9   consequences for community assembly and ecosystem functioning. *Annals of Botany* 1-8.

10 Dwyer JM, Laughlin DC. 2017. Constraints on trait combinations explain climatic drivers of

11   biodiversity: the importance of trait covariance in community assembly. *Ecology Letters* 20:

12   872-882.

13 Enquist BJ, Kerkhoff AJ, Stark SC, Swenson NG, McCarthy MC, Price CA. 2007. A general

14   integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*

15   449: 218-222.

16 Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences.

17   *Statistical Science* 7: 457-511.

18 Griffith DM, Veech JA, Marsh CJ. 2016. Cooccur: Probabilistic species co-occurrence analysis

19   in R. *Journal of Statistical Software* 69: 1-17.

20 Hart SP, Schreiber SJ, Levine JM. 2016. How variation between individuals affects species

21   coexistence. *Ecology Letters* 19: 825-838.

1   HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking

2   community assembly through the lens of coexistence theory. *Annual Review of Ecology,*

3   *Evolution, and Systematics* 43: 227-248.

4   Hoffmann WA, Poorter H. 2002. Avoiding bias in calculations of relative growth rate. *Annals of*

5   *Botany* 80: 37-42.

6   Hutchinson GE. 1961. The paradox of the plankton. *The American Naturalist* 95:1 37-145.

7   Kraft NJB, Godoy O, Levine JM. 2015. Plant functional traits and the multidimensional nature of

8   species coexistence. *Proceedings of the National Academy of Sciences USA* 112: 797-802.

9   Laughlin DC, Messier J. 2015. Fitness of multidimensional phenotypes in dynamic adaptive

10   landscapes. *Trends in Ecology and Evolution* 30: 487-496.

11   Laughlin DC, Strahan RT, Adler PB, Moore MM. 2018. Survival rates indicate that correlations

12   between community-weighted mean traits and environments can be unreliable estimates of

13   the adaptive value of traits. *Ecology Letters* 21: 411-421.

14   Li Y, Jiang Y, Shipley B, et al. 2021. The complexity of trait-environment performance

15   landscapes in a local subtropical forest. *New Phytologist* 229: 1388-1397.

16   MacArthur R, Levins R. 1967. The limiting similarity, convergence, and divergence of

17   coexisting species. *The American Naturalist* 101: 377-385.

18   Marks CO, Lechowicz MJ. 2006. Alternative designs and the evolution of functional diversity.

19   *The American Naturalist* 167: 55-66.

20   McElreath R. 2016. *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*.

21   Boca Raton: Chapman & Hall/CRC.

22   McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006. Rebuilding community ecology from

23   functional traits. *Trends in Ecology and Evolution* 21: 178-185.

1   Mohan JE, Clark JS, Schlesinger WH. 2007. Long-term CO_2 enrichment of a forest ecosystem:

2   implications for forest regeneration and success. *Ecological Applications* 17: 1198-1212.

3   Onoda Y, Westoby M, Adler PB, et al. 2011. Global patterns of leaf mechanical properties.

4   *Ecology Letters* 14: 301-312.

5   Pérez-Ramos IM, Matías L, Gómez-Aparicio L, Godoy Ó. 2019. Functional traits and

6   phenotypic plasticity modulate species coexistence across contrasting climatic conditions.

7   *Nature Communications* 10: 2555.

8   Pistón N, de Bello F, Dias ATC, et al. 2019. Multidimensional ecological analyses demonstrate

9   how interactions between functional traits shape fitness and life history strategies. *Journal of*

10   *Ecology* 107: 2317-2328.

11 Poorter H, Remkes C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing

12   in relative growth rate. *Oecologia* 83: 553-559.

13 Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to

14   leaves, stems and roots: meta-analyses of interspecific variation and environmental control.

15   *New Phytologist* 193: 30-50.

16 R Development Core Team. 2016. R: A language and environment for statistical computing. R

17   Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

18 Reich PB. 2014. The world-wide "fast-slow" plant economics spectrum: a traits manifesto.

19   *Journal of Ecology* 102: 275-301.

20 Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: Global convergence in plant

21   functioning. *Proceedings of the National Academy of Sciences USA* 94: 13730-13734.

22 Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M. 2006. Jack of all trades, master of

23   some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981-993.

1 Stan Development Team. 2020. RStan: the R interface to Stan. R package version 2.19.3.

2   http://mc-stan.org.

3 Swenson NG, Worthy SJ, Eubanks D, et al. 2020. A reframing of trait-demographic rate analyses

4   for ecology and evolutionary biology. *International Journal of Plant Sciences* 181: 33-43.

5 Tilman D .1982. *Resource competition and community structure*. Princeton: Princeton University

6   Press.

7 Turcotte MM, Levine JM. 2016. Phenotypic plasticity and species coexistence. *Trends in*

8   *Ecology and Evolution* 31: 803-813.

9 Umaña MN, Zhang C, Cao M, Lin L, Swenson NG. 2015. Commonness, rarity, and intraspecific

10   variation in traits and performance in tropical tree seedlings. *Ecology Letters* 18: 1329-1337.

11 Umaña MN, Zipkin EF, Zhang C, Cao M, Lin L, Swenson NG. 2018. Individual-level trait

12   variation and negative density dependence affect growth in tropical tree seedlings. *Journal of*

13   *Ecology* 106: 2446-2455.

14 Veech JA. 2013. A probabilistic model for analyzing species co-occurrence. *Global Ecology and*

15   *Biogeography* 22: 252-260.

16 Worthy SJ, Laughlin DC, Zambrano J, et al. 2020. Alternative designs and tropical tree seedling

17   growth performance landscapes. *Ecology* 101: e03007.

18 Wright IJ, Reich PB, Westoby M, et al. 2004. The worldwide leaf economics spectrum. *Nature*

19   428: 821-827.

20 Wright IJ, Westoby M. 1999. Differences in seedling growth behavior among species: trait

21   correlations across species, and trait shifts along nutrient compared to rainfall gradients.

22   *Journal of Ecology* 87: 85-97.

1   Wright SJ. 2002. Plant diversity in tropical forests: a review of mechanisms of species

2   coexistence. *Oecologia* 130: 1-14.

3   Yang J, Cao M, Swenson NG. 2018. Why functional traits do not predict trait demographic rates.

4   *Trends in Ecology and Evolution* 33: 326-336.

5   Yang J, Song X, Cao M, et al. 2020. On the modeling of tropical tree growth: the importance of

6   intra-specific trait variation, non-linear functions and phenotypic integration. *Annals of*

7   *Botany* 127: 533-542.

8   Zirbel CR, Brudvig LA. 2020. Trait-environment interactions affect plant establishment success

9   during restoration. *Ecology* 101: e02971.
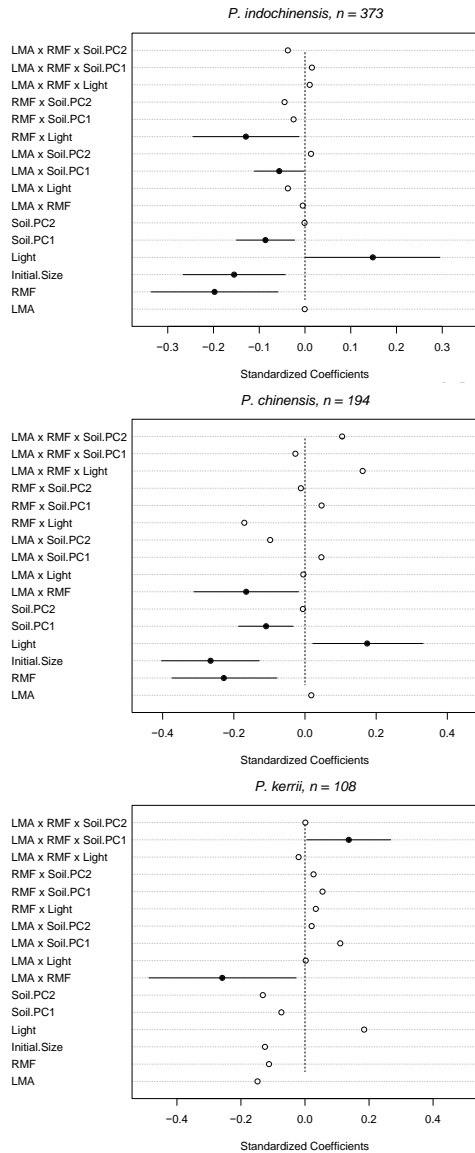
Figure 1. Standardized regression coefficients for each of the three species in the study for models examining the relationships between traits, environmental variables, and their interactions on seedling relative growth rate. Circles represent posterior mean values and filled circles indicate significant effects. Lines representing 95% credible intervals are only presented for significant effects to minimize the x axis and allow better viewing. All variables were natural log-transformed and scaled to unit variance. PC1 scores are negatively associated with K, Mg and Zn and PC2 scores are negatively associated with Ca and P.

33
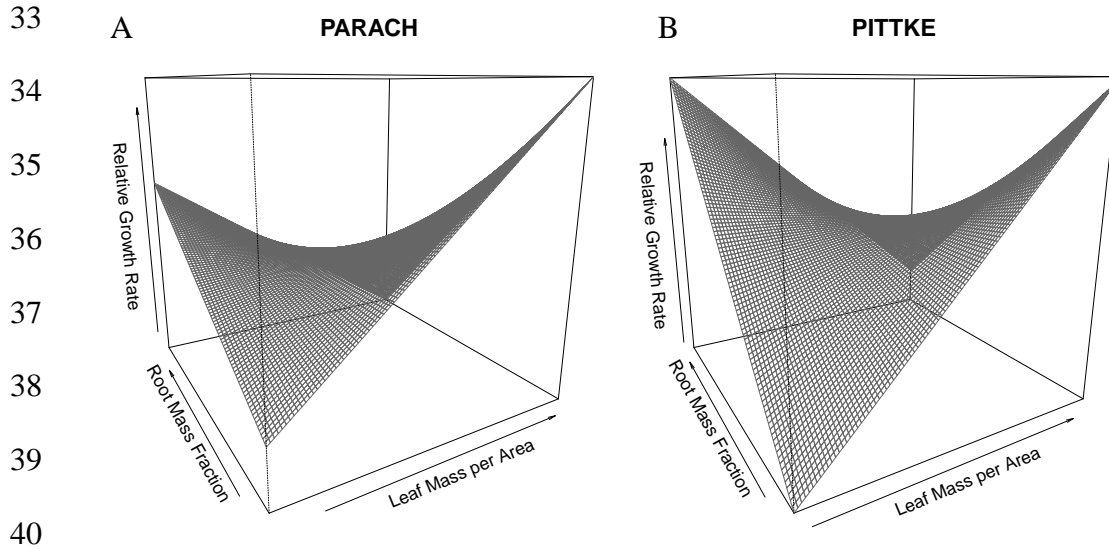
Figure 2. *P. chinensis* (PARACH, 194 individuals) and *P. kerrii* (PITTKE, 108 individuals) each had a significant two-way interaction between leaf mass per area (LMA) and root mass fraction (RMF) showing evidence of intraspecific trait combinations. For both species, PARACH **(A)** and PITTKE **(B)**, individuals had higher relative growth rate (RGR) when they had high LMA and low RMF, but also had higher RGR when they combined low LMA with high RMF.
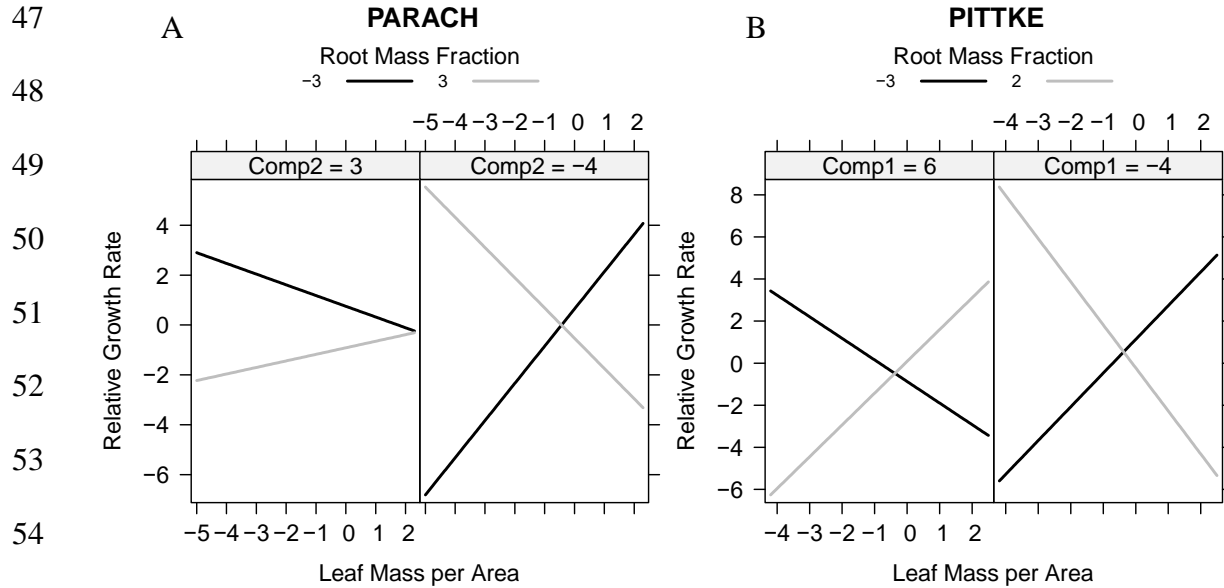
Figure 3. *P. chinensis* (PARACH, 194 individuals) and *P. kerrii* (PITTKE, 108 individuals) each had a significant three-way interaction between leaf mass per area (LMA), root mass fraction (RMF) and one of the soil nutrient principal components. **(A)** For PARACH, the interaction was between LMA, RMF, soil component 2 (Comp2). The low soil environment of soil component 2 has high levels of Ca and P due to its negative association with these minerals. At the poor nutrient, high value end of the soil variable, (Comp2 = 3) individuals had higher relative growth rate (RGR) when they combined low LMA with low RMF. At the high nutrient end of the soil variable (Comp2 = -4), there were two peaks in RGR, one for individuals that combined high LMA with low RMF and one for individuals that combined low LMA with high RMF. **(B)** For PITTKE, the interaction was between LMA, RMF, and soil component 1 (Comp1). The low soil environment of soil component 1 has high levels of Mg, K and Zn due to its negative association with these minerals. At the high end of the soil gradient (Comp1 = 6), which corresponds to low nutrient levels, individuals had higher RGR when they combined high LMA with high RMF or low LMA with low RMF. At the opposite end of the gradient (Comp1 = -4) with high soil

27

70   nutrients, there were two peaks in RGR, one for individuals with high LMA and low RMF and

71   one for individuals with low LMA and high RMF. All variables were scaled and natural log-

72   transformed.