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Using plant-soil feedbacks to predict plant biomass in diverse communities

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Abstract. It has become clear that plants can create soils that affect subsequent plant growth. However, because plant-soil feedbacks (PSFs) are typically measured in monoculture experiments, it remains unclear to what extent PSFs affect plant growth in communities. Here we used data from a factorial PSF experiment to predict the biomass of 12 species grown in 162 plant community combinations. Five different plant growth models were parameterized with either monoculture biomass data (Null) or with PSF data (PSF) and model predictions were compared to plant growth observed in communities. For each of the five models, PSF model predictions were closer to observed species biomass in communities than Null model predictions. PSFs, which were associated with a 28% difference in plant biomass across soil types, explained 10% more variance than Null models. Results provided strong support for a small role for PSFs in predicting plant growth in communities and suggest several reasons that PSFs, as traditionally measured in monoculture experiments, may overestimate PSF effects in communities. First, monoculture data used in Null models inherently includes "self" PSF effects. Second, PSFs must be large relative to differences in intrinsic growth rates among species to change competitive outcomes. Third, PSFs must vary among species to change species relative abundances.

Key words: coexistence; community assembly; competition; facilitation; model; pathogen; prediction; soil; symbiont.

INTRODUCTION

Plant soil feedbacks (PSFs) have gained attention for their potential role in determining plant growth and coexistence (Kardol et al. 2006, Bever et al. 2010, van der Putten et al. 2013). However, rather than directly testing the effect of PSFs in plant communities, most PSF research uses data from monoculture pot experiments and results from theoretical models to infer the importance of PSFs to plant growth in communities (Hawkes et al. 2013, Revilla et al. 2013, Baxendale et al. 2014). For example, PSF studies typically measure monoculture plant growth on "self-" and "other-"cultivated soils. Greater growth on "self" than on "other" soils is defined as a positive PSF, whereas greater growth on "other" than "self" soils is defined as a negative PSF. Results from theoretical models are used to infer that positive PSFs will result in competitive exclusion and negative PSFs will result in coexistence through species replacements (Bever 1994, Bever et al. 1997, Kulmatiski and Kardol 2008).

There are several potential problems with assuming that results from "self" vs. "other" PSF experiments are important for plant growth in communities. First, it is not clear that PSFs measured in monoculture experiments are realized in plant communities (Shannon et al. 2012, Baxendale et al. 2014, Hilbig and Allen 2015, Jing et al. 2015). Second, most "self" vs. "other" experimental approaches ignore the fact that PSFs are likely to differ among "other" soil types, so for example, a plant may realize a negative PSF relative to one soil type, and a positive PSF relative to another soil type (Kos et al. 2015). The extent to which these soil-type-specific PSFs occur and whether they are important in plant communities is not known because the factorial experiments needed to test for soil-type-specific PSFs are rarely performed (Casper et al. 2008, Kulmatiski et al. 2011). Third, the importance of PSFs to plant growth is usually inferred from theoretical model results, but theoretical models often assume competitive equivalence among plant species; this assumption is typically not valid in natural plant communities (Bever 1994, Eppstein and Molofsky 2007, Petermann et al. 2008, Turnbull et al. 2010, Kulmatiski et al. 2011, Suding et al. 2013). As a result, despite a growing number of studies that demonstrate that plants can create soils that change subsequent plant growth, for several reasons, it is not clear whether typical PSF values are relevant to how plants grow in communities (van der Putten et al. 2013, Burns and Brandt 2014).

Some of the strongest evidence that PSFs may be important to plant communities comes from research

showing a correlation between PSFs and plant abundance in communities (Klironomos 2002, Mangan et al. 2010, Lankau et al. 2011, Anacker et al. 2014), but this type of research is rare. Further, a more direct test for the role of PSFs is possible. By parameterizing PSF models with and without PSF effects and comparing model predictions to plant growth observed in plant communities, it is possible to assess the importance of PSFs relative to null models (Petermann et al. 2008, Turnbull et al. 2010, Kulmatiski et al. 2011, 2012, Burns and Brandt 2014).

Here we develop five simple plant growth models that can be implemented with or without PSF data. The five models include an Additive Model (Loreau and Hector 2001), an Exponential Model (Kulmatiski et al. 2011), and three logistic models that differed in their expectation of carrying capacity (Kulmatiski et al. 2011). We parameterize these models either with plant growth data from monoculture pots (i.e., Null models) or with data from a factorial PSF experiment, where each species was grown on soils from each of the other species in a community (i.e., PSF models). We compare model predictions to plant biomass observed in 162 plant communities comprised of two to 12 plant species grown in a greenhouse.

Methods

Factorial PSF experiment

Greenhouse experiments were conducted at the USDA-ARS Forage and Range Research Laboratory in Logan, Utah, USA. PSFs were determined for 12 species common to Temple, Texas, USA and used in previous studies (Wilsey and Polley 2004, Wilsey and Wayne Polley 2006, Isbell et al. 2009). These species included the C4 grasses *Bouteloua curtipendula* (BC), *Bothriochloa ischaemum* (BI), *Bothriochloa saccharoides* (BS), *Panicum coloratum* (PC), *Sporobolus asper* (SA), *Sorghastrum nutans* (SN), and *Schizachyrium scoparium* (SS); the C3 grass *Nassella leucotricha* (NL); and the C3 forbs *Echinacea purpurea* (EP), *Oenothera speciosa* (OS), *Ratibida columnifera* (RC), and *Salvia azurea* (SC). We did not, however, use *Paspalum dilatatum* because seeds for this non-native, invasive C4 grass were difficult and unethical to collect and transport. A standard two-phase "self" vs. "other" PSF experimental approach was used (Bever 1994, Kulmatiski and Kardol 2008, Brinkman et al. 2010). Many PSF studies compare the growth of a species on "self-cultivated" (henceforth "self") soils to the growth of the same species on soils cultivated by various "other" species. In some studies soils cultivated by several non-self species are mixed to create an "other" soil. In other studies a target plant may be grown in one replicate pot of Species B cultivated soil, in a second replicate pot of Species C cultivated soil and so on. These nonfactorial "self" vs. "other" approaches require few replicate pots and provide information on how plants

grow on "other" soils in general but do not provide reliable information about how a target species grows on the soil of every other potential species in a community. We used a factorial design that measured the growth of each plant species on soils cultivated by every other species. For example, for Plant A we measured growth on replicate pots of Plant A soils, Plant B soils, Plant C soils, etc. (Kulmatiski and Kardol 2008).

In Phase I of the experiment, 2,220 pots (20 cm height) were filled with 1 L of steam-sterilized growth medium (a mixture of 6:1 sand and peat moss) that was inoculated with 50 mL (5% by volume) field soil from Temple, Texas, USA (Wilsey and Polley 2004). Field soils (0–20 cm) were collected under dry conditions (July) from one 3 × 3 m area in a field previously used for experiments with the target species (Wilsey and Polley 2004). Collected soils were homogenized by hand prior to mixing with the growth medium. Each of the 12 target species were planted into 185 replicate pots (i.e., 12 × 185 = 2,220). Four germinated seeds were planted in each pot. After 1 week, each pot was weeded to include the two largest individuals. Plants were grown for three months then harvested. At the beginning of Phase II, 16 mL of Hoagland solution was added to each pot to compensate for nutrients lost as a result of plant harvesting, minimize plant-nutrient feedbacks, and isolate plant-microbe feedbacks (Bever 1994). In Phase II, four germinated seeds from each plant species were planted in 185 pots: 20 with "self" soils and 15 with soils from each of the other 11 species. After 1 month in Phase II, each pot was weeded to include the two largest individuals. After three months in Phase II, aboveground biomass was harvested, dried to constant weight at 70°C, and weighed.

Community greenhouse experiment

As in the first experiment, a 6:1 sand to peat mix with 5% field inoculum was used to fill 198, 12 L pots. Three replicate monocultures of each of 12 species were planted in 36 pots. Randomly selected but unique 2-, 4-, and 8-species communities were assigned to 45, 45, and 52 pots, respectively. Finally, 20 replicate pots were assigned to 12-species communities. In each pot, 48 germinated seeds were planted and after one week the least vigorous individuals of each species were removed so that all pots had 24 individuals and an equal number of individuals per species after removals. After four months, aboveground biomass was harvested, dried to constant weight at 70°C, and weighed by species.

PSF calculations

Final biomass values from the factorial PSF experiment were used to calculate 132 *PSF* values: one *PSF* value for each species on each "other" species' soil type. For example, species A would have one *PSF* value for soils created by species B and another *PSF* value for soils created by species C. *PSF* values were calculated as the

difference in growth for a target plant on "self" and "other" soils divided by the maximum growth for a target plant on "self" and "other" soils: $PSF_A\beta = [(A_\alpha - A_\beta)/\max(A_\alpha, A_\beta)]$ (Table 1; Markham and Chanway 1996, Kulmatiski and Kardol 2008, Brinkman et al. 2010). *PSF* values can vary from −1 for species that do not grow on "self" soils to +1 for species that do not grow on "other" soils. If species A grew to 10 g on "self" soil and to 15 g on soil type β, then species A would have a $PSF_A\beta$ value of −0.33 [i.e., (10–15)/(15) = −0.33].

To test the role of PSFs, we rely primarily on the ability of plant growth models to predict plant growth in communities (described herein), but we also developed a simple index to determine how often the factorial experiment produced PSF effects large enough to change competitive outcomes between species pairs. This index is the difference in the growth of a plant species on two soil types divided by the difference in growth between two species: [i.e., $(A_\alpha - A_\beta)/(A_\alpha - B_\beta)$; Table 1]. When plant growth differs more between two soil types than between two plant species in a way that changes competitive outcomes, this test returns values > 1. When plant growth differs more between two species than between two soil types, this test returns values < 1. To determine if the factorial experiment produced more values greater than 1 than would be produced by a typical "self" vs. "other" PSF experiment, we replaced 'plant growth on soil type β' with 'mean plant growth on all "other" soil types' [i.e., $(A_\alpha - \overline{A_{\beta..t}})/(A_\alpha - B_\beta)$] where $\overline{A_{\beta..t}}$ is the mean growth of plant A on all "other" soils.

Model development

The first model, the Additive model, was used because it is a simple model that has been used in related research

that aimed to predict plant biomass in communities (Loreau and Hector 2001). We used this model to provide a simpler alternative to the remaining time-specific models. The exponential model follows that of Bever et al. (1997) and was used in similar PSF research by the authors (Kulmatiski et al. 2011, 2012). The remaining three logistic models were developed to "control" runaway growth that occurs in exponential models. This was important in this experiment because data from the 3-month PSF experiment were used to predict plant growth in communities that were grown for four months. Three different logistic models were used to explore the effects of different carrying capacities on model predictions. This ensemble of models allowed comparison to results from previous research (exponential model), to test different approaches to controlling exponential growth (additive vs. logistic models) and, more generally, allowed us to explore the effects of PSFs across a range of modeling approaches that may be used in future research. Each model was parameterized either with plant monoculture data on control soils (i.e., Null models) or with monoculture data from each soil type (i.e., PSF models). Control soils were defined as soils that had not been cultured by a target plant species.

The Additive model provides a facile approach to estimating community composition and biomass based only on standing plant biomass (Loreau and Hector 2001). The Null version of this model simply scales the maximum plant biomass observed in monoculture pots (from the community greenhouse experiment) by its proportion of the community [i.e., $\max(A_{ctrl})/N_j$] where N_j = the number of species in community *j*. If Plant A grew to a maximum of 5 g in a monoculture pot, then Plant A would be predicted to produce 1 g of biomass in a 5-species community. A PSF version of this model was created by multiplying Null Additive model predictions by community-specific *PSF* values {i.e., $[(1\text{-}CPSFj) \times Max(A_{ctrl})]/N_j$}. Community-specific PSF values were calculated as the mean of *PSF* values for the species in the community. Plant growth values [$max(Actrl)$] were multiplied by 1-*CPSF* values because negative PSF values are predicted to result in overyielding in communities and positive PSF values are predicted to result in underyielding in communities. (Kulmatiski et al. 2012). This model was parameterized using the maximum growth observed across monoculture pots in the community experiment. Mean or median biomass could similarly be used.

The remaining four models were time-specific and similar to previously published PSF models (Kulmatiski et al. 2011, 2012). These models are based on three premises: each plant species cultivates a soil type, the growth of each soil type is a function of the abundance and growth of the plant that cultivates it, and each plant grows at a rate that is specific to each soil type (Bever 1994, Kulmatiski et al. 2011).

The Exponential Model is described in Kulmatiski et al. (2012). In this model, plant growth rates are a

TABLE 1. Parameters definitions for Null and plant-soil feedback models.

Parameter	Definition
$A_t, B_t, ..., I_t$	Biomass of plants A–I at time *t*
$A\alpha, A\beta, ..., A\iota$	Biomass of plant A on soil types α to ι
α, β, ..., ι	Biomass of soil types associated with plants A–I
$\Gamma_A, \Gamma_B, ..., \Gamma_\iota$	Growth rates of plants A–I
$\Gamma_A\alpha, \Gamma_{A\beta}, ..., \Gamma_{A\iota}$	Plant A's growth rate on soil types α to ι
κ_{commx}	Carrying capacity of a community *x*
$\kappa_A, \kappa_B, ..., \kappa_I$	Carrying capacity of plants A–I
A_{ctrl}	Monoculture biomass of plant A on control soils
$P_{\alpha t}$	Proportion of soil type A at time *t*
$PSF_A\beta$	Plant-soil feedback value for species A on soil type β
$CPSF_x$	Plant-soil feedback value for a species in community *x*
μ	Conversion factor for microbial biomass growth rates

function of the proportional abundances of each soil type. However, in contrast to previous continuous-time models (Bever 2003, Levine et al. 2006, Eppstein and Molofsky 2007, Kulmatiski et al. 2011), this model used a discrete-time approach that provides specific estimates of plant and soil type biomass (e.g., A_t and α_t; Table 1). The growth of plant biomass A at time-t is assumed exponential given by $A_{t+1} = (1 + \Gamma_{At})A_t$ where the growth parameter is a linear combination of exponential growth rates on all soil types, weighted by the proportion of soil-type present, i.e., $\Gamma_{At} = (\Gamma_{A\alpha}P_{A\alpha} + \Gamma_{A\beta}P_{A\beta} + \Gamma_{A\gamma}P_{A\gamma} +...)$. Similarly, growth for a particular soil type is assumed exponential, and the growth rate is a function of the biomass of the plant creating that soil type, i.e., $\alpha_{t+1} = (1 + \mu\Gamma_{A\alpha}A_t)\alpha_t$ (Table 1). Soil type biomass is typically assumed to represent microbial biomass (Bever et al. 1997) and by setting the parameter μ to 5, we assume that microbial growth rates are greater than plant growth rates (Kulmatiski et al. 2011). When parameterized with the same data, this model produces quantitatively similar results to the analogous continuous-time version of the model (Kulmatiski et al. 2011).

The third model (the Logistic Species-Level-K Model) uses a logistic form of the Exponential model where $A_{t+1} = A_t + \Gamma_A A_t((\kappa_A - A_t)/\kappa_A)$ (Table 1). Carrying capacity (κ) in the Logistic Species-Level-K model was defined as the maximum biomass observed for each species across "self" pots in the Community experiment (κ_i or species-specific κ). In this model each plant's growth is limited only by the carrying capacity of that species; plant growth is not affected by the amount of growth of other plants in the community.

To account for the growth of other plants in the community, the fourth model (the Logistic Pot-Level-K model) was calculated as follows: $A_{t+1} = A_t + \Gamma_A A_t \{[\kappa_A - (A_t + B_t + C_t +...)]/\kappa_A\}$. This model assumes that each plant's growth is limited by a species-specific κ (κ_A) and total plant growth in the community (i.e., $A_t + B_t + C_t +...$).

Finally, because carrying capacity can have an overriding effect on final biomass, the fifth model (the Logistic Constant-K Model) replaced the species-specific κ (κ_i) in the Logistic Pot-Level-K Model with a pot-level K (κ_{commx}), which was set as the mean pot biomass + 2SD observed across all plant communities in the community greenhouse experiment.

For each of the four time-specific growth models, plants were assumed to start growth as seed (0.002 g) and time-step-specific growth rates were calculated for 40 time steps as $(^{40}\sqrt{F/I}) - 1$, where F = final biomass and I = initial biomass (Kulmatiski et al. 2012). Growth rates were calculated from the 3-month PSF experiment and used to model four months of plant growth in the Community experiment. Each of the 40 time-steps, therefore, represented 2.25 d so models were run for 53 time steps to represent the 4-month growth period in the Community experiment, unless otherwise noted.

Statistical analyses

Factorial PSF experiment.—To determine if biomass differed among species in the factorial PSF experiment, a one-factor generalized linear mixed model (GLMM) was used with species as the fixed effect. To determine if biomass differed by soil type, a one-factor GLMM was used with soil type as the fixed effect; analyses were performed by species because we were not interested in species by soil type comparisons. Transformations to meet assumptions of homogeneity and normality were used as necessary. For all tests, a post-hoc Tukey–Kramer method was used to adjust for Type I error and determine pairwise differences among least square means. Means from raw data are reported.

Comparing model predictions to observed species and community biomass.—To determine if PSF data improved Null model predictions across species, a Student's t-test on the absolute difference between observed and predicted values for the Null and PSF models was conducted. To determine the goodness-of-fit between observed and predicted values, a Pearson correlation coefficient was calculated and reported as an R^2 value. Correlation P values are reported and considered significant when $P < 0.05$; however, we compare R^2 values between models regardless of significance because if we assume a nonsignificant correlation explains no variance, the variance explained by a significant model is overestimated. We also use R^2 values to explain both the absolute variance explained by different models as well as the percent of unexplained variance explained by each model. For example, if Null and PSF model predictions produce R^2 values of 0.6 and 0.8, respectively, then the PSF model is described as explaining 20% of the total variance (i.e., 0.8 – 0.6) and 50% of the unexplained variance (i.e., 1–0.6 = 0.4 and 0.2/0.4 = 0.5 or 50%) relative to the Null model.

To test if PSF and Null model predictions of each species' biomass differed from each other and from observed values, a one-factor GLMM was used with "data source" (i.e., observed data, Null model predictions or PSF model predictions) as the fixed effect and species-level biomass as the response variable. Correlation, t-test and mixed model analyses were computed using the CORR, TTest and GLIMMIX procedures, respectively in SAS/STAT for Windows, Release 9.2 (SAS Institute Inc., Cary, North Carolina, USA).

Results

Greenhouse experiments

Plant biomass differed among soil types for five of the 12 species tested (i.e., demonstrated PSFs; Appendix S1: Table S1). In each case, plants grew better on "self" than "other" soils. More specifically, mean *PSF* values across soil types for *B. curtipendula*, *B. ischaemum*, *O. speciosa*, *R. columnifera* and *S. azurea* were 0.38, 0.25, 0.69, 0.54

and 0.38, respectively (Appendix S1: Table S2). When *PSFs* were calculated regardless of statistical differences among soil types, 10 of 12 species demonstrated positive *PSFs* (Appendix S1: Table S2). Only *S. asper* and *S. scoparium* demonstrated negative *PSFs* and these effects were small (i.e., mean *PSF* across soil types were −0.10 and −0.01, respectively). Across species, the coefficient of variation of plant biomass among soil types was 0.29. Plant biomass also differed by plant species ($F_{11,1867}$ = 42.53, P < 0.001; Table 2, Appendix S1: Table S3). Across species, the coefficient of variation of plant biomass among plant species was 0.50. Mean biomass values of each species on each soil type (Appendix S1: Table S1) were used to parameterize models regardless of statistical significance.

Though, on average, biomass varied more by plant species than by soil type, in 33 of 132 pairwise comparisons plant biomass differed more by soil type than by species in a way that would change competitive outcomes (Appendix S1: Table S4). When the same test was performed using a mean "other" value instead of soil-type-specific values, there were only 14 of 132 pairwise comparisons where soil effects were larger than differences in intrinsic growth rates.

Model predictions

PSF-informed model predictions were closer to observed plant biomass than Null model predictions for each model individually and when data from all five models were combined (Fig. 1, Table 3; Appendix S1: Fig. S1). Predictions from two of five Null models (i.e., the Logistic species-level-K and Logistic pot-level-K) were correlated with observed biomass (Fig. 1, Table 4). In contrast, predictions from four of five PSF models were correlated with observed biomass (all except the Exponential; Fig. 1, Table 4). Across all models, PSF models explained 10% more total variance than Null models. With the exception of the Additive model, PSF models explained 2–8% more total variance than the Null models (Table 4). This 2–8% of total variance represented 11–16% of the variance unexplained by Null models. PSFs had a greater effect on the Additive model where PSFs explained 32% more total variance and 67% of the variance unexplained by Null models.

PSF had the greatest effect on predictions of the Additive model. Null Additive model predictions were not significantly correlated with observed values, but

PSF Additive model predictions provided some of the best correlations with observed values (Fig. 1, Table 4). PSF Additive model predictions differed from Null model predictions for four of 12 species (*B. curtipendula, O. speciosa, P. coloratum* and *R. columnifera*; Fig. 1A; Appendix S1: Table S5). Two of these species-level responses were consistent across models in that PSF model predictions for *O. speciosa* and *R. columnifera* were smaller than Null model predictions for each of the five models (Fig. 1). This reflected the fact that these two species had the largest positive PSF values (i.e., 0.69 and 0.54, respectively; Appendix S1: Table S2); positive PSFs result in underyielding in the PSF model (Kulmatiski et al. 2012). Other species-level differences between Null and PSF model predictions were *B. curtipendula* and *S. asper* in the Exponential model and *B. curtipendula* in the Logistic Species-Level-K model (Fig. 1).

The Additive model was parameterized using the maximum observed biomass of species monocultures in large pots (i.e., A_{ctrl}). Alternative biomass values such as mean biomass in large monoculture pots or mean biomass in small pots from the first phase of the PSF experiment would have produced qualitatively similar results (i.e., PSF data improved correlations from 0.23 to 0.63 and from 0.20 to 0.31, respectively) but are not discussed further.

The Exponential model produced some of the worst predictions of species biomass in communities (Fig. 1B). This occurred despite the fact that we ran the Exponential model for 40 time steps (reflecting the length of time of parameterization) rather than the 53 time steps that the observed communities were grown. When run for 53 time steps, the PSF predictions were still closer to observed values than Null predictions (R^2 = 0.58 and 0.51, respectively) but predictions greatly overestimated total plant biomass (i.e., by 2,500% for the Null model; data not shown), emphasizing the importance of including carrying capacity in these models.

When run for 53 time steps, Null and PSF Logistic Species-Level-K model predictions were similarly correlated to observed species biomass (R^2 = 0.5 for both models) but predictions greatly overestimated total biomass (i.e., by 1,700% for the Null model). This logistic model overestimated total biomass because individual species growth rates were not affected by other species in the pot. To allow this model to produce more reasonable biomass estimates, the Logistic Species-Level-K model was run for 40 time steps. When this adjustment was made, both Null

TABLE 2. Mean plant species biomass (± 1 SE). Species names followed by different lower case letters in parentheses are different at the alpha = 0.05 level. Species names reported in the *Methods* section.

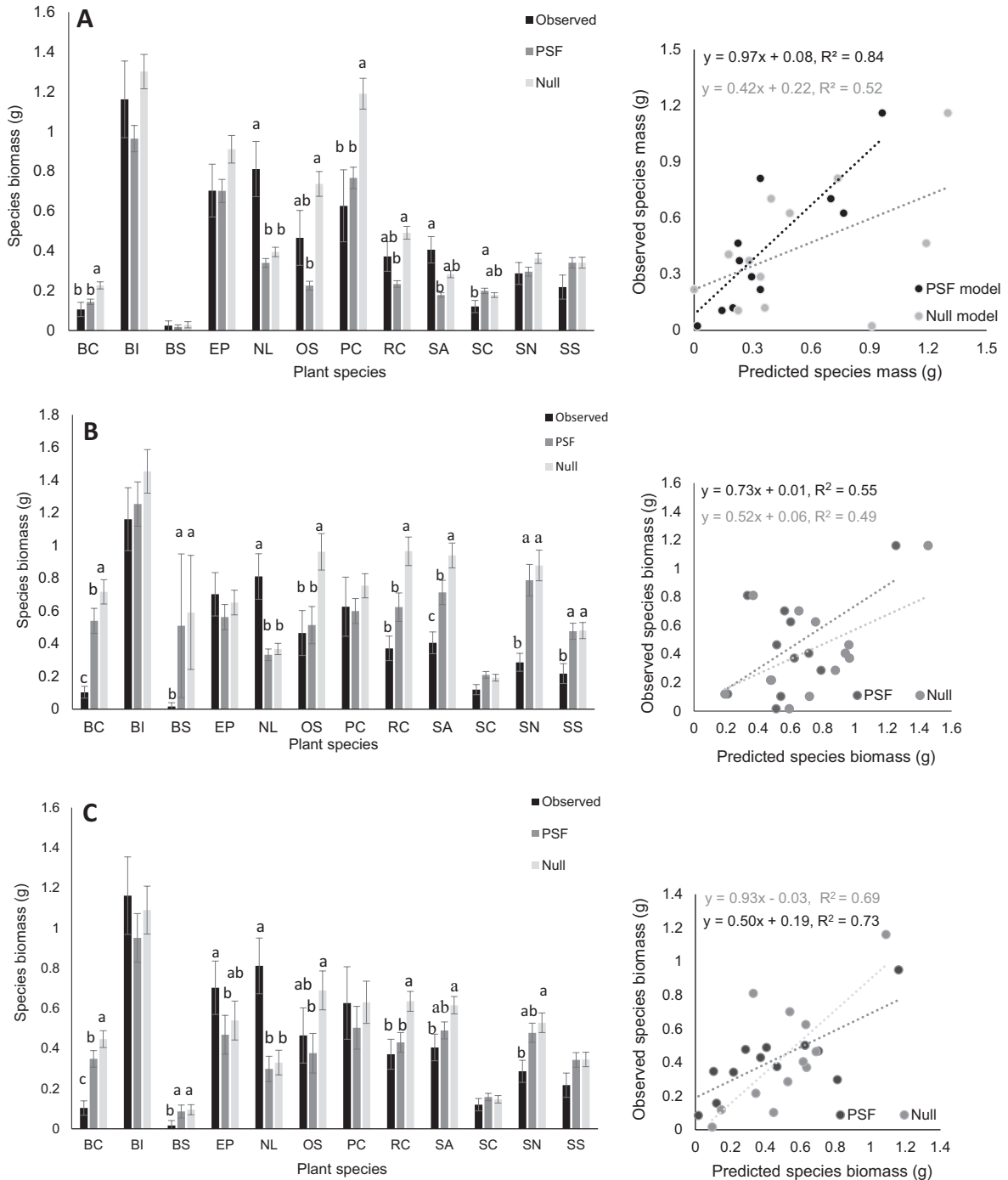|	Plant species											
	BC (d)	BI (a)	BS (de)	EP (de)	NL (e)	OS (e)	PC (d)	RC (cd)	SA (bc)	SC (e)	SN (b)	SS (d)
Biomass (g)	0.13 (0.01)	0.29 (0.01)	0.10 (0.01)	0.15 (0.01)	0.08 (0.01)	0.10 (0.01)	0.13 (0.01)	0.15 (0.01)	0.18 (0.01)	0.06 (0.00)	0.19 (0.01)	0.13 (0.01)

FIG. 1. Observed and modeled plant biomass for 12 species grown in 162 plant communities. Five models [Additive (A), Exponential (B), Logistic Species-level-K (C), Logistic Pot-level (D) and Logistic Constant-K (E)] were parameterized either with monoculture data (Null) or with plant-soil feedback data (PSF). Lower case letters indicate differences among observed, Null and PSF values for each species. A linear regression and R^2 of observed vs. predicted values is shown (Inset). See *Methods* section for species codes, Table 4 for regression statistics and Appendix: Table S5 for ANOVA results.

and PSF model predictions were similar to and correlated with observed plant biomass (Fig. 1C).

The Logistic Pot-Level-K model constrained total plant growth in a pot and was run for 53 time steps. This

model produced the highest correlations between predicted and observed results of both the Null and PSF models: both Null and PSF versions of this model were correlated with observed values. Finally, the Logistic
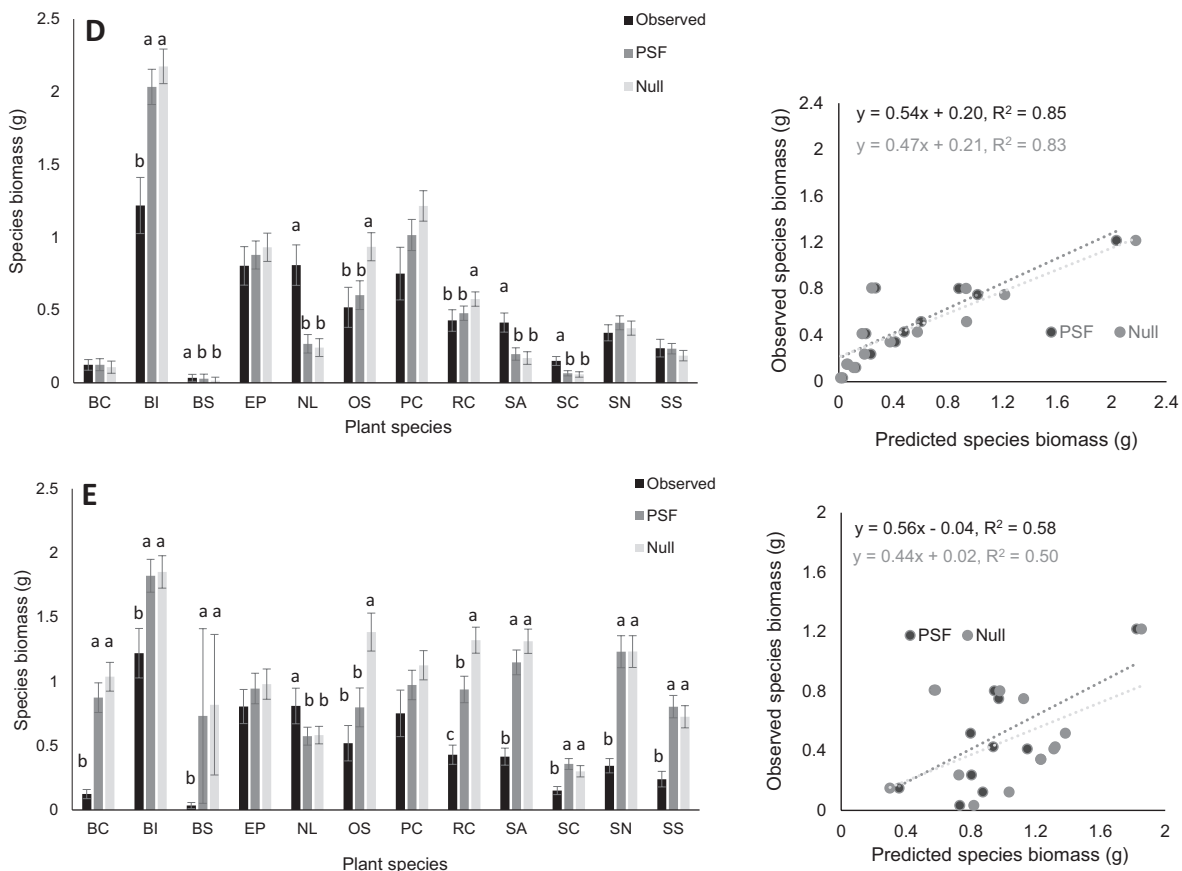
Fig. 1 Continued.

TABLE 3. Student's *t*-test statistic on the absolute difference between observed and predicted species biomass for the Null and PSF models. The degrees of freedom is 11 for each test.

Model	T-statistic	P
Additive	3.50	**0.005**
All models	7.85	**<0.001**
Exponential	3.72	**0.003**
Logistic species level-K	3.51	**0.005**
Logistic pot-level-K	2.66	**0.022**
Logistic constant-K	4.29	**0.001**

Constant-K model also constrained total plant growth in a pot and was run for four months (Fig. 1E; Appendix S1: Table S5). Only the PSF model predictions for this model were correlated with observed values; however, this model did not perform as well as the other Logistic PSF models.

DISCUSSION

PSF research rarely tests the extent to which PSFs measured in monocultures are associated with plant growth in communities (van der Putten et al. 2013). In this study, for each of five plant growth models tested, PSFs improved predictions of species biomass measured in plant communities. PSF-informed models explained 2–32% more total variance than Null models, though the largest effects were only observed in the Additive model. In the four discrete-time models, PSF-informed models explained 2–8% more total variance than Null models and this represented 11–16% of unexplained variance. This was smaller but similar to a previous study in which the Exponential PSF model explained 17% more total variance and 26% of unexplained variance relative to the Null Exponential model (Kulmatiski et al. 2011). In both studies, improved correlations reflected many small improvements in species biomass predictions rather than a few large improvements. Results, therefore, provided clear support for a small role for PSFs in determining plant biomass in plant communities.

PSF research often relies on nonfactorial experimental designs that ignore the fact that a plant may grow well on soil type B and poorly on soil type C. A factorial PSF experiment not only indicates how much plant growth varies among "other" soil types but also indicates when plant growth differs more by soil type than by plant type.

TABLE 4. Pearson correlation coefficients (R^2) and associated P values for the relationship between observed species biomass and Null and PSF model predictions, respectively. The difference in R^2 values between Null and PSF models (R^2 difference) and the percentage of variance unexplained by Null models that was explained by PSF models (% explained by PSFs) is shown.

Model	N	Null model		PSF model		R^2 difference	% explained by PSFs
		R^2	P	R^2	P		
Additive	12	0.515	0.086	**0.838**	**<0.001**	0.32	67
All models	60	**0.560**	**<0.001**	**0.620**	**<0.001**	0.06	14
Exponential	12	0.489	0.107	0.547	0.066	0.06	11
Logistic species level-K	12	**0.687**	**0.014**	**0.727**	**0.007**	0.04	13
Logistic pot-level-K	12	**0.825**	**0.001**	**0.846**	**<0.001**	0.02	12
Logistic constant-K	12	0.500	0.098	**0.579**	**0.049**	0.08	16

This is important because it determines when PSF effects are large enough to overcome differences in intrinsic growth rates between species. In 33 of 132 pairwise comparisons, PSFs were large enough to change competitive outcomes between species pairs (Appendix S1: Tables S1 and S4). In contrast, using a nonfactorial "self" vs. "other" approach with the same data indicated 14 of 132 pairwise comparisons where PSFs were large enough to change competitive outcomes. This is the only study we are aware of that has performed a factorial PSF experiment with more than five species and results suggest that, relative to the nonfactorial design, the factorial design detects more than twice as many instances where PSF effects are greater than differences in intrinsic growth rates (Casper and Castelli 2007, Lankau et al. 2011, Hawkes et al. 2013).

Parameterizing growth models with experimental data revealed an obvious but overlooked effect of competitive inequality on PSF: plants with little biomass have small effects on PSFs in a community. For example, in this study, *B. ischaemum* grew very poorly on *B. curtipendula* and *S. azurea* soils resulting in relatively large PSF values of 0.46 on both soil types. However, because *B. curtipendula* and *S. azurea* never had high biomass in communities, they had little effect on model predictions of *B. ischaemum* growth in communities. One implication is that a small PSF for a large plant can have a greater effect on model predictions of community composition and biomass than a large PSF for a small plant. Another implication is that "self" soils will be more important in determining the growth of large (or dominant) species than small (or rare) species simply because soils cultivated by large species will be more abundant than soils cultivated by small species (Petermann et al. 2008, Turnbull et al. 2010). Similarly, "other" soils will be more important to small species than large species (but see; Peltzer et al. 2009). More broadly, plant size or abundance can have a large effect on how PSFs are realized in a community.

In this study, PSFs were associated with a mean 28% difference in growth on different soils, yet PSFs only explained 2–8% more variance than Null time-specific models. We suggest several reasons that relatively large PSF effects will cause relatively small improvements in predictions of plant mass in communities. First, Null models include plant growth data from "self" soils. As noted earlier, large plants are less affected by "other" soils than small plants so PSF and Null model predictions for large plants are not likely to differ as much as for small plants. Consistent with this, a post-hoc test revealed that the difference between Null and PSF model predictions, as a proportion of maximum predicted plant biomass, decreased with plant size (i.e., PSFs had a greater effect on smaller plants; $F_{1,11} = 4.91$; $P = 0.05$, $R^2 = 0.32$). Second, PSFs must be comparable in size to differences in intrinsic growth rates among species to affect rank order abundance (Petermann et al. 2008, Turnbull et al. 2010, Kulmatiski et al. 2011, Revilla et al. 2013, Sun et al. 2014). For example, PSF will not be important to two plants if Plant A grows to between 8 and 10 g on soils A-D and Plant B grows to between 1 and 4 g on soils A-D. For these two species, there is no case in which Plant B will outcompete Plant A, regardless of the size of PSF. Third, PSFs must be variable among species to affect relative abundances. If all plants in a community have a −0.5 PSF , then the relative abundances of species would be determined by fitness differences and not PSF; whereas, if some plants have a PSF of −0.5 while other plants have a PSF of −0.1, then there is an opportunity for PSF effects to counteract fitness differences. Finally, our models that included carrying capacity limited PSF effects because growth rates had relatively small effects on the biomass of plants that approach carrying capacity. Modeling approaches that incorporate PSF into carrying capacities could address this problem.

It is notable that while PSFs improved predictions of plant biomass in this experiment, results are unlikely to provide insight into plant growth in the field. Plant growth in this experiment was not correlated with the abundance of the same species in previous field experiments ($F_{1,11} = 0.57$, $P = 0.47$, $R^2 = 0.05$; Wilsey and Polley 2004). Further, most PSFs in this experiment were positive, whereas most PSFs reported across the literature are negative (Kulmatiski et al. 2008). It is likely that different experimental conditions, such as more nutrient- or microbial-rich soils, water stress or

soil compaction, would have produced more negative PSFs or species abundances that were more similar to field experiments (Kyle et al. 2007, Casper et al. 2008). Results therefore highlight the potential that PSF may vary quantitatively and qualitatively as a function of experimental conditions and as a result inference to the landscape is likely to require field experiments (Casper et al. 2008).

While PSFs improved predictions for all five models tested, PSFs had the smallest effect in the best performing model—the Logistic Pot-Level K model. We suggest that although PSF effects were very small in the best model in this study, it is appropriate to consider PSF effects across the ensemble of models used here because (1) PSFs have demonstrated consistent improvements in predictions across a range of model assumptions and experiments (Petermann et al. 2008, Mangan et al. 2010, Kulmatiski 2011, van der Putten et al. 2013) and (2) future studies are likely to use a variety of models and experimental conditions and it is not clear which model will perform best in other experimental conditions (Larios and Suding 2014). The fact that the simple PSF Additive model performed as well as the Logistic Pot-Level K model supports this suggestion.

While PSF effects were small relative to the effect of differences in intrinsic growth rates, results were consistent with the idea that PSFs exert widespread effects on plant growth and community development, because PSFs produced many small improvements in predictions of species biomass across a wide range of community compositions. Further, the magnitude of PSF effects in this study were similar or smaller than PSF effects reported across the literature suggesting that PSFs in other communities will have similar or larger effects on community composition (Kulmatiski et al. 2008). PSF effects may also be stronger in long-term field experiments or with different species assemblages (Petermann et al. 2008, Turnbull et al. 2010, Hawkes et al. 2013, Mack and Bever 2014, Maron et al. 2014). Where PSFs are important to plant growth, there is potential for improved understanding, prediction and management of plant communities (Lortie et al. 2004, Kulmatiski 2011, Lankau et al. 2011, Nolan et al. 2015, Storkey et al. 2015).

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