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Fine-root traits are linked to species dynamics in a successional plant community

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Abstract. Despite the importance of fine roots for the acquisition of soil resources such as nitrogen and water, the study of linkages between traits and both population and community dynamics remains focused on aboveground traits. We address this gap by investigating associations between belowground traits and metrics of species dynamics. Our analysis included 85 species from a long-term data set on the transition from old field to forest in eastern North America (the Buell-Small Succession Study) and the new Fine-Root Ecology Database. Given the prominent roles of life form (woody vs. non-woody) and species origin (native vs. exotic) in defining functional relationships, we also assessed whether traits or their relationships with species dynamics differed for these groups. Species that reached their peak abundance early in succession had fine-root traits corresponding to resource acquisitive strategies (i.e., they were thinner, less dense, and had higher nitrogen concentrations) while species that peaked progressively later had increasingly conservative strategies. In addition to having more acquisitive root traits than native species, exotics diverged from the above successional trend, having consistently thinner fine roots regardless of the community context. Species with more acquisitive fine-root morphologies typically had faster rates of abundance increase and achieved their maximal rates in fewer years. Decreasing soil nutrient availability and increasing belowground competition may become increasingly strong filters in successional communities, acting on root traits to promote a transition from acquisitive to conservative foraging. However, disturbances that increase light and soil resource availability at local scales may allow acquisitive species, especially invasive exotics, to continue colonizing late into the community transition to forest.

Key words: functional traits; root diameter; root nitrogen content; root tissue density; species dynamics; species invasions; specific root length; successional dynamics.

Introduction

Despite the theoretical importance of soil resource acquisition strategies in determining plant competitive outcomes and successional dynamics (Tilman 1985), trait-based studies of changes in species abundance have largely focused on aboveground characters such as seed mass, specific leaf area, and rates of gas exchange (Weiher et al. 1999, Diaz et al. 2004). Such approaches have yielded critical insights into ecological processes such as succession (Garnier et al. 2004, Fukami et al. 2005, Douma et al. 2012) and plant invasion (Tecco et al. 2010, van Kleunen et al. 2010, Mozdzer and Caplan 2018), but the strong aboveground bias has meant that inferences do not necessarily encompass the full range of trait-mediated dynamics. Investigations focusing on root traits explicitly could therefore yield additional insight into the means by which belowground foraging strategies influence species dynamics.

Variation in fine-root traits can often be described on the basis of shifts in resource foraging that range from acquisitive (i.e., roots that are cheaply constructed but proliferate and acquire resources more rapidly) to conservative (i.e., roots that require greater investment and live longer, but acquire resources more slowly; Freschet et al. 2010, Kong et al. 2014, Reich 2014, Roumet et al. 2016). Although trait patterns of fine roots have greater dimensionality than do those of leaves (e.g., due to interactions with mycorrhizal fungi; Weemstra et al. 2016), several key relationships have been identified. For example, larger diameter roots and higher root tissue density

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(RTD) are both associated with greater tissue construction costs and longer average fine-root lifespans, reflecting a more conservative strategy (McCormack et al. 2012, Reich 2014). Conversely, roots with greater nitrogen (N) content and higher specific root length (SRL) are typically associated with greater respiration rates and lower construction costs, reflecting a more acquisitive strategy. While mycorrhizal fungi also play an important role in nutrient foraging, plant associations with mycorrhizal fungi can be partly inferred from root diameter in both woody and non-woody species (Kong et al. 2014, Li et al. 2017, Ma et al. 2018). Assessments of root functional traits can therefore provide insight into species-level resource foraging strategies and adaptation to a given soil environment (Comas and Eissenstat 2004, Liu et al. 2015, Chen et al. 2016, Caplan et al. 2017).

Successional dynamics result in a complex suite of changes in growth conditions for plant species over time. At least in the ideal case, the expectation is a transition from high to low resource availability, and low to high competition for those resources, as succession proceeds (Tilman 1985, Vitousek and Reiners 1991). Community composition can therefore be expected to change though succession such that acquisitive species dominate initially but are gradually replaced by more conservative species. While studies have used aboveground functional traits to purportedly establish that successional communities adhere to this expectation (Garnier et al. 2004, Rasmann et al. 2011, Douma et al. 2012), these studies have not evaluated plant root traits directly.

Belowground, large parts of a successional community may deviate from the expected transition from acquisitive to conservative species. This could occur, for example, due to high niche complementarity among species or functional groups (Mommer et al. 2010). It is also possible that shifts in resource availability aboveground may be decoupled from those belowground (e.g., due to nutrient deposition, bioturbation, or other disturbances), facilitating nutrient acquisitive species at nearly any point in succession (Carson and Pickett 1990, Davis et al. 2000, Erktan et al. 2018). In particular, those acquisitive species with novel life histories or ecological interactions (such as positive plant–soil feedbacks or low pathogen loads) may be able to achieve high abundance even late in succession. As these ecological circumstances pertain to many exotic species (Ehrenfeld et al. 2005, Blumenthal et al. 2009), fine-root traits and their relationship with species' successional positions may contribute to patterns of invasion.

Plant functional traits are known to influence population sizes and how they change through time (hereafter "species dynamics"; Keddy 1992, Fukami et al. 2005, Li et al. 2015). Although stochastic processes and immigration can also influence abundance patterns, functional traits translate into increased abundance when they increase organismal-level survival, growth, reproduction, and dispersal under favorable environmental and biotic conditions (Poorter et al. 2008, Wright et al. 2010, Adler et al. 2014). Therefore, root trait expressions that confer effective soil resource uptake strategies at different phases of succession can be expected to covary with metrics of species dynamics. In particular, species with acquisitive trait expressions (e.g., high SRL and root N) may be expected to reach their peak abundance in early successional communities (when resource availability is high) and species that have more conservative trait expressions (e.g., larger diameter and RTD) may be more likely to peak in abundance as resource availability decreases over time. Moreover, the rate and timing of abundance increase, as well as the maximum abundance achieved, may shift in accordance with the acquisitive to conservative transition.

Although soil resource acquisition is conceptually important in the ecological sorting of species during succession and in influencing species dynamics, restricted availability of root trait data has precluded empirical analyses of these relationships. Here, we overcome this limitation by coupling a recently released database synthesizing several decades worth of fine-root trait observations (Iversen et al. 2017*b*) with a long-term data set on old-field succession (Meiners et al. 2015*b*). Combining these data sets, we explicitly connect species' root traits with their dynamics to identify functional linkages suggested by other studies (Li et al. 2015, Caplan et al. 2017). Specifically, we hypothesized that (1) species that reach their peak abundance early in succession have root traits corresponding to resource acquisitive strategies, while species that peak progressively later have increasingly conservative strategies. We further hypothesized that (2) among common species, exotic species exhibit more acquisitive root traits than native species, with this difference being greatest for species that peak late in succession. In investigating the above, we also evaluated whether the shift in dominance from herbaceous to woody species during succession plays a role in defining shifts in belowground strategies through the course of succession. Finally, we hypothesized that (3) interspecific variation in fine-root traits would be linked with species' temporal dynamics. We expected more acquisitive species to exhibit greater maximal rates of abundance increase, to achieve those rates more quickly, and to reach greater peak abundance levels, with highly conservative species exhibiting the opposite; we also expected exotics to outperform natives across all metrics.

METHODS

Species dynamics data

Data on plant species dynamics (Data S1) came from the Buell-Small Succession Study (BSS), located within the Hutcheson Memorial Forest Center in the Piedmont region of New Jersey, USA (40°30′ N, 74°34′ W). The BSS has documented the successional transition of plant communities (Appendix S1: Fig. S1) in 10 former agricultural fields that were experimentally abandoned in pairs between 1958 and 1966 (Myster and Pickett 1990, Meiners et al. 2015*a*). A prior study at the site suggests that soil nutrient concentrations declined as the community aged (Robertson and Vitousek 1981) and a strong increase in tree cover through the mid-successional portion of the study (Appendix S1: Fig. S1a) indicates that light availability followed a similar trend.

The 10 fields of the BSS are contiguous and range in size from 0.5 to 1.0 ha; size varies with the position of fields along the border with an adjacent old-growth forest. Each field contains 48, 1-m^2, permanent plots whose vegetation was inventoried annually each July until 1979 and biennially thereafter; during inventories, the percent cover of all species in each plot was recorded. The data used here come from inventories that took place during the first 58 yr of the study. The data set makes possible quantitative, though not individual-based, comparisons of species dynamics through analyses of trends in plant cover and the frequency of plots colonized, approximating population dynamics (Meiners 2007). Cover-based measures from the BSS are more strongly influenced by the growth of individual plants and clonal expansion, whereas frequency-based measures are more conservative but more closely reflect the spread of individuals (Meiners et al. 2009). We assessed both types of data in this analysis to capture the range of species dynamics possible. Given that the BSS has documented a complete series of life form transitions spanning short-lived herbaceous communities to young forests, the data set encapsulates a wide range of ecological conditions under which gradients of traits and associated resource acquisition strategies could potentially manifest.

We extracted species dynamics information for the 85 species in the BSS data set for which root trait data were also available (Appendix S2: Tables S1, S2). This equates to 27% of the 311 species that have been documented at the site and 36–60% of cover (interannual mean = 45%; Appendix S1: Fig. S2). All species were angiosperms and the vast majority formed arbuscular mycorrhizae (a group for which fine-root traits and mycorrhizal colonization are well correlated; Li et al. 2017, Ma et al. 2018). Most of the species were relatively abundant at some point in the successional transition. Before proceeding, data were aligned by field age to account for differences in the calendar year of field abandonment. We then summed field-level cover or plot occurrence values across the 10 fields (but within ages) and divided these by the total plot area or number of plots inventoried, respectively. This approach generated composite trajectories of species abundance that we could relate to fine-root traits and allowed us to include species that were insufficiently abundant to yield reliable field-level species dynamics estimates. From the aligned data set, we used the maximum frequency and cover of each species across all possible ages (i.e., peak frequency and cover, or P_{f} and P_{c}, respectively) and the successional age at which each species reached its peak (we define this as a species' successional position, SP; Appendix S1: Fig. S3). We included data at the genus level for *Vitis* spp. and *Carex* spp. This was done because species within these genera are not differentiable in the field, either due to their location in the tree canopy (*Vitis*) or infrequent flowering (*Carex*), and was viable because congeneric species present within the BSS are ecologically similar.

Additional metrics of species dynamics, namely the maximum rate of abundance increase (or "maximum expansion rate," μ) and the time until this rate was reached (or "rise time," δ), were determined in cases where they could be reliably determined (60–77% of species; Appendix S2: Tables S1, S2). We specifically included species that had at least 5 yr of data and for which P_{f} exceeded 1.0% or P_{c} exceeded 0.1% (percentages are relative to the total number of inventoried plots or their areas, respectively). To identify the remaining species' most prominent rise in plot frequency or cover, we first fit frequency or cover data with smoothing splines (R function smooth.spline, $\gamma = 0.0001$). We then identified all periods of appreciable rise within smoothed data by identifying spans for which the first derivative of the spline remained positive for ≥6 yr; we retained those whose linear slope was ≥10% of the maximum found for each species (Appendix S1: Fig. S3). For all remaining periods of frequency or cover increase, we determined (1) the maximum rate of cover or frequency increase (denoted μ_{c} and μ_{f}, respectively) using the first derivative of the spline and (2) the number of years between the onset of the rise and the age at which μ occurred (denoted δ). From the set of parameter pairs for each species (typically ≤3), the maximum value of μ and the corresponding δ were retained; we presumed they correspond to the abundance rise that occurred when environmental conditions were closest to optimal for the species. SP was used to determine if and how fine-root traits are associated with species' successional position (i.e., to test the first two hypotheses), while μ, δ, and P were used to determine how fine-root traits correspond to metrics of species' temporal dynamics (i.e., to test the third hypothesis).

Root trait data

Data on fine-root traits (Data S1) were obtained primarily from the Fine-Root Ecology Database version 1.0 (FRED; Iversen et al. 2017*a*). Data from two additional studies (Jo et al. 2015, Caplan et al. 2017) were also included to increase the representation of shrubs. FRED is a publicly available database containing both species-specific and community level data on fine-root traits from sites across the globe. Root trait data therefore did not come from the BSS site specifically, though most of the studies FRED contains on BSS species were conducted in northeastern North America. Furthermore, previous studies indicate that, compared to leaves, roots often express stronger within-taxa conservatism (Comas and Eissenstat 2009, Kong et al. 2014, Valverde-Barrantes et al. 2017) and comparatively low within-species plasticity (Freschet et al. 2015), but this is not universal (Freschet et al. 2017, Iversen et al. 2017*b*).

We applied several selection criteria to the records in FRED to maximize the relevance and consistency of the data used in our analysis. We first removed all records for dead or necrotic roots, as well as those measured on young plants (<10 d), as developing roots can have different trait values than mature roots. Next, we excluded records for coarse roots (i.e., those >2 mm in diameter), mixed fine and coarse roots, and those for which the functional designation was not specified or ambiguous. Finally, we excluded data collected on the basis of root branching order or that represented a subset of the <2 mm pool. This left records pertaining strictly to the traditional definition of fine roots (<2 mm in diameter). Although other means of classifying fine roots exist (McCormack et al. 2015), none are yet as widely used. Using the <2 mm definition therefore maximized both the size and consistency of the data set used in our analysis. Preliminary analyses were conducted on data from only first-order roots, and results were similar to those reported here.

We focused on four core fine-root traits: specific root length (SRL, m/g), mean root diameter (mm), root tissue density (RTD, g/cm^3), and root N content (N, mg/g). These traits relate to tissue construction costs and resource acquisition efficiency and are among the most well-represented traits in FRED. While diameter and RTD are mathematically related to SRL, woody and non-woody species often express greater variation in diameter and RTD, respectively, such that the three traits together provide greater insight into patterns of root construction than any one trait can alone. For the traits considered, FRED typically contained one to six records from one to three studies for a given species in the BSS (Appendix S2: Table S2), with data in most records derived from 3–10 replicate plants. Numbers were substantially higher for the most common species and in cases where studies included multiple sampling locations, time points, or experimental treatments; each combination of species and location, time point, or treatment comprised a separate record in FRED.

Initially, our fine-root data set described 33–55 species per trait but we expanded this to 85 species for all traits (Appendix S2: Tables S1, S2) using Bayesian hierarchical probabilistic matrix factorization (BHPMF; Shan et al. 2012, Fazayeli et al. 2014, Schrodt et al. 2015). Briefly, we provided the full FRED database (3,577 trait records for 802 species) and taxonomic information at multiple levels to a BHPMF algorithm, which filled data gaps across the entire data set at the record level (see Appendix S3 for details). From the resulting data set, we extracted the (now complete) records for the 85 species and two genera (i.e., *Vitis* and *Carex*) that met our criteria for inclusion. To determine how gap-filling affected the results, we computed species-level trait values for both the original and gap-filled data sets; these were calculated as geometric means of all pertinent records for each species (i.e., observations and estimates) using log-transformed data.

Species considerations

Species names were matched between BSS and FRED after standardizing taxonomy to The Plant List 1.1 (The Plant List 2010) with the R package taxonstand (Cayuela et al. 2012). Higher-order taxonomy (i.e., genus, family, order, and group) for all species were obtained using the R package taxonlookup 1.1.1 (Pennell et al. 2016). The status of species with respect to life form (woody vs. non-woody) and origin (native vs. exotic) was determined from Gleason and Cronquist (1991) and joined to the combined demography and fine-root data set (Data S1).

Our analysis focused on common species, in part because our hypotheses were more likely to apply to them, but also because data on fine-root traits are far more abundant for common species (Appendix S2: Table S2). Moreover, our determination of μ and δ required species to generate persistent and expanding populations over an extended period of time ($\geq$6 yr); species that remained at low abundance in the BSS could not be analyzed. In effect, we therefore focused on species that could be described as aggressive or invasive (Richardson et al. 2000, Colautti and MacIsaac 2004), though we applied the same criteria to both native and exotic taxa. Consistent with this, all of the exotic woody species included have been identified as regionally invasive in eastern North America and many of the natives included are invasive in Eurasia. Likewise, many of the herbaceous taxa in the species pool are considered invasive in North America and/or Eurasia.

Statistical analysis

We evaluated predictions of the first and second hypotheses together using linear models. To determine if species' fine-root traits became more conservative as their successional positions (SP) occurred progressively later (our first hypothesis), we modeled data on root traits, which were response variables in separate models, as a function of either the age of peak cover (SP_c) or plot frequency (SP_f). To determine if fine-root traits differed between exotic and native species with the difference increasing in species peaking progressively later (our second hypothesis), we included terms for Origin and the SP × Origin interaction, respectively, in each of the eight linear models. Trait data were $\log_{10}$-transformed to improve residual normality and homoscedasticity. We conducted two analyses to determine if life form (i.e., woody vs. non-woody status; we denote the corresponding model term "Form") could explain potential shifts in root traits as a function of successional position. We first computed variance inflation factors with SP and Form entered into a single model and then repeated the above analyses replacing terms for SP with terms for Form.

The evaluation of linkages between metrics of species dynamics and fine-root traits (i.e., predictions of our third hypothesis) used a similar linear modeling approach to that described above. However, metrics of species dynamics (P, μ, and δ) were used as response variables, and fine-root traits were used as predictor variables. Trait data were again $\log_{10}$-transformed. To determine if the evaluated relationships were consistent for native and exotic species, we included terms for Origin and the Trait × Origin interaction in all models.

We fit linear models using the original (i.e., not gap-filled) root trait data set in parallel with the above analyses. Results were highly consistent with those arising from the gap-filled data set; results based on the strictly empirical data set are provided in Appendix S2: Tables S3-S5. The significance of terms in all models was determined using F statistics computed from type II sums of squares ($\alpha = 0.05$). All analyses were performed using R version 3.4.0 (R Development Core Team 2017). If appropriate, post hoc evaluations (e.g., differences in means between origins but within life forms) were conducted using least-squares means via the R package lsmeans (Lenth 2016).

RESULTS

Successional trends

Data for all four root traits were consistent with the first hypothesis, namely that species' fine-root traits would transition from acquisitive to conservative through the course of succession (Fig. 1, Table 1). Approximately linear relationships were found whether successional position was determined from cover or plot frequency data. For SRL, the pooled trend (i.e., native and exotic species combined) entailed a decline of ~76% in species that peaked early in the successional series as compared to species that peaked towards the end (Fig. 1a, b). Further, root N content declined across the range of successional positions by 40% (Fig. 1g, h), whereas increases occurred for both root diameter (by 42%; Fig. 1c, d) and RTD (by 82%; Fig. 1e, f).

The relationship between species' root traits and successional positions corresponded, in large part, to that between traits and life form. In evaluating models containing terms for both SP and Form (not shown), variance inflation factors ranged from 11.9 to 40.1, indicating that these variables were collinear (Graham 2003). Further, statistical evaluations yielded consistent outcomes whether a species' life form or the successional age at which it peaked was included as the explanatory variable (Tables 1 and 2). Specifically, declines in SRL and N with increasing SP were paralleled by lower values for woody than non-woody species (Fig. 2a, d; Table 2). Likewise, the increase in diameter and RTD with SP was paralleled by greater values for woody vs. non-woody species (Fig. 2b, c).

Differences by origin

In support of our second hypothesis, exotic species had more acquisitive root trait values than native species for two of the four traits evaluated (Tables 1 and 2). Specifically, exotics produced fine roots that, on average, were thinner and had higher SRL (Figs. 1 and 2). However, RTD did not differ among species on the basis of origin and N was greater in native vs. exotic species. Patterns were consistent across woody and non-woody species for SRL, RTD, and N (Fig. 2a, c, d), whereas mean diameter only differed by origin for woody species (Fig. 2b). Origin explained a similar portion of the variation in SRL to that explained by SP ($\eta \approx 0.20$), though it explained less variation in N than did SP (e.g., $\eta_{\text{origin}} = 0.08$ vs. $\eta_{\text{SP}} = 0.15$); these results were consistent for frequency- and cover-based data sets (Table 1).

There was partial support for the prediction that exotics and natives would diverge more strongly for species peaking in abundance later in succession. Specifically, the SP × Origin interaction was significant in the case of fine-root diameter (Table 1) corresponding to native species having thicker fine roots with increasing SP while exotics had relatively thin fine-root diameters regardless of their position (Fig. 1c, d). There was also a nonsignificant trend in the SRL vs. SP relationships wherein exotics appeared to decline less steeply through the successional transition than did natives (Fig. 1a, b).

Relationships with species dynamics

Our results presented modest support for the prediction of our third hypothesis that temporal dynamics would be associated with fine-root traits. When calculated from plot frequency data, maximum rates of abundance increase (μ_f) were greater for species with higher SRL (Fig. 3a) and smaller fine-root diameter (Fig. 3b; Table 3). In both cases, root traits explained a modest portion of the variation in μ_f ($\eta = 0.073$ and 0.082), in large part due to non-woody species with relatively acquisitive trait values spanning wide ranges in μ_f. We found no evidence that these relationships differed between native and exotic species or that μ_c was associated with the traits evaluated (Table 3). Three ruderal herbaceous species had particularly high μ_f: *Fragaria virginiana* (6.48%/yr), *Daucus carota* (6.16%/yr), and *Alliaria petiolata* (6.15%/yr).

The number of years required for species to reach their maximum rates of frequency increase (δ_f, or "rise time") was correlated with all fine-root traits but diameter, with more acquisitive values associated with shorter rise times (Fig. 3c–e; Table 3). When calculated on the basis of cover, rise time (δ_c) was correlated with all four traits (Table 3; Appendix S1: Fig. S4). There was a notable outlier in the relationship for δ_f; the rise time for *Celastrus orbiculatus* (54 yr) was far longer than that of any

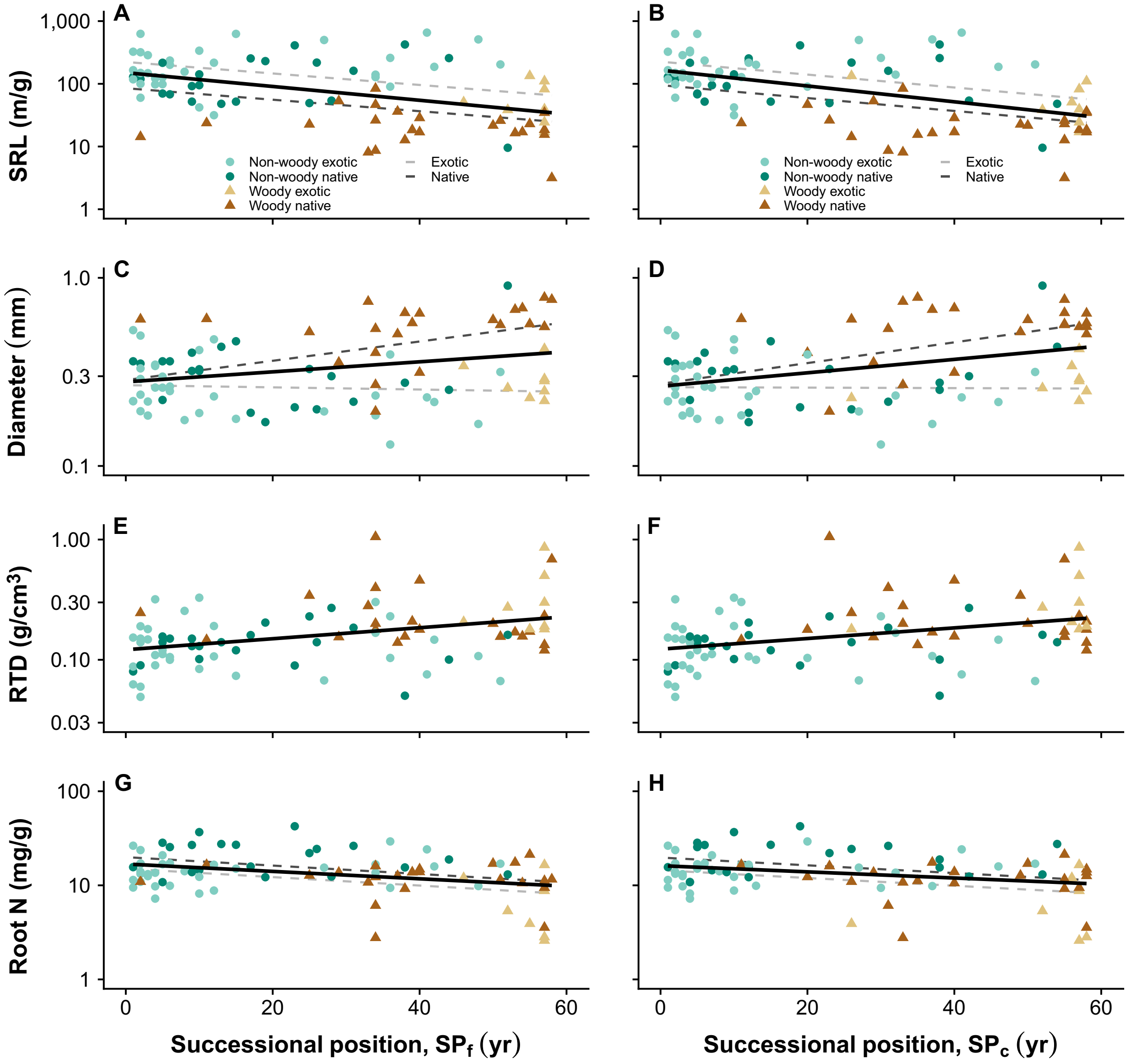

FIG. 1. Correspondence between fine-root traits and successional position; each point represents a species. Successional position is given as the age at which the species reached its peak (A, C, E, G) plot frequency or (B, D, F, H) cover. Solid lines show trends irrespective of species origin while dashed lines show differences by origin if terms for Origin or Trait × Origin were significant (Table 1). Symbol color and shape denote plant form while saturation denotes origin; symbols in all panels are as indicated in panels A and B. Note that all y-axes are shown on log scales. SRL, specific root length; diameter, mean diameter of fine roots; RTD, root tissue density; root N, nitrogen concentration in root tissue.

other species. Inspection of its frequency trajectory indicated that it had spread at a highly linear rate (~1.5%/yr) for at least two decades but that it accelerated slightly in the last few years of the data set.

The final metric of species dynamics we considered, peak abundance, exhibited a significant correlation with root N when calculated on the basis of frequency (Table 3). However, the nature of this relationship diverged between exotic and native species (i.e., the Trait × Origin interaction was significant), with root N being slightly greater in native species with larger peak frequencies (P_f) but substantially lower in exotic species with larger P_f (Fig. 3f). Two exotic species with notably low root N concentrations and high peak frequencies appeared to be disproportionately influential in defining this relationship; these were the lianas *Celastrus orbiculatus* and *Lonicera japonica*.

DISCUSSION

Successional trends

Our first hypothesis, that root traits would transition from acquisitive to conservative as species' peak

TABLE 1. Statistical results for models of fine-root traits as a function of successional position and species origin (native vs. exotic).

	Frequency				Cover			
Trait and term	η	*F*	df	*P*	η	*F*	df	*P*
SRL								
SP	**0.17**	**16.3**	**1,80**	**<0.001**	**0.22**	**22.5**	**1,80**	**<0.001**
Origin	**0.21**	**21.3**	**1,80**	**<0.001**	**0.18**	**17.4**	**1,80**	**<0.001**
SP × Origin	0.04	3.5	1,80	0.063	0.04	3.4	1,80	0.067
Diameter								
SP	**0.05**	**4.6**	**1,80**	**0.035**	**0.10**	**9.2**	**1,80**	**0.003**
Origin	**0.25**	**26.4**	**1,80**	**<0.001**	**0.22**	**23.0**	**1,80**	**<0.001**
SP × Origin	**0.12**	**10.5**	**1,80**	**0.002**	**0.12**	**11.3**	**1,80**	**0.001**
RTD								
SP	**0.12**	**11.0**	**1,80**	**0.001**	**0.12**	**10.5**	**1,80**	**0.002**
Origin	0.01	0.8	1,80	0.377	0.00	0.4	1,80	0.543
SP × Origin	0.01	0.4	1,80	0.524	0.01	0.6	1,80	0.444
Root N								
SP	**0.15**	**14.4**	**1,80**	**<0.001**	**0.13**	**12.2**	**1,80**	**0.001**
Origin	**0.08**	**6.7**	**1,80**	**0.011**	**0.09**	**7.7**	**1,80**	**0.007**
SP × Origin	0.00	0.1	1,80	0.769	0.00	0.0	1,80	0.960

Notes: See Fig. 1 for abbreviations of root traits; SP, successional position, defined as the age at which the species reached its peak cover or frequency. η values are proportional to the fraction of variation in the response variables (root traits) explained by each term.

Values for significant model terms are shown in bold.

TABLE 2. Statistical results for models of fine-root traits as a function of life form (woody vs. non-woody) and species origin (native vs. exotic).

Trait and term	η	*F*	df	*P*
SRL				
Form	**0.46**	**68.6**	**1,80**	**<0.001**
Origin	**0.13**	**12.2**	**1,80**	**0.001**
Form × Origin	0.01	1.1	1,80	0.295
Diameter				
Form	**0.20**	**20.5**	**1,80**	**<0.001**
Origin	**0.17**	**16.9**	**1,80**	**<0.001**
Form × Origin	**0.08**	**6.7**	**1,80**	**0.011**
RTD				
Form	**0.26**	**28.8**	**1,80**	**<0.001**
Origin	0.00	0.1	1,80	0.814
Form × Origin	0.02	1.7	1,80	0.195
Root N				
Form	**0.33**	**39.6**	**1,80**	**<0.001**
Origin	**0.18**	**17.5**	**1,80**	**<0.001**
Form × Origin	0.01	1.1	1,80	0.305

Notes: See Fig. 1 for abbreviations of root traits. η values are proportional to the fraction of variation in the response variables (root traits) explained by each term.

Values for significant model terms are shown in bold.

abundance levels occurred progressively later in succession, was supported for all four of the root traits examined. Belowground shifts in resource acquisition strategies through succession thus mimic those seen aboveground in the BSS. Seed mass and leaf dry matter content both increase as species peak later in succession (Meiners et al. 2015*b*), reflecting the necessity for greater allocation to offspring support and increased leaf retention in later successional environments (Westoby et al. 1992, Navas et al. 2010, Douma et al. 2012). Given that biotically mediated changes in environmental conditions during succession can affect fundamental processes including nutrient mineralization, photosynthesis, and plant regeneration, covariation among these disparate aspects of plant function should perhaps be expected (Navas et al. 2010). These changes may occur relatively rapidly, as observed in our study, or may be the result of long-term changes in soil fertility that drive changes in fine-root traits (Holdaway et al. 2011). Nonetheless, our results provide root-centric evidence that species replacement in succession predominantly tracks greater resource scarcity belowground, as it does aboveground (Garnier et al. 2004, Rasmann et al. 2011, Douma et al. 2012). By extension, changing soil and light regimes through the course of succession and the associated shifts in competitive dynamics (Faillace et al. 2018) may act as parallel filters on species' abilities to increase in abundance at any point in the successional process.

Phylogenetic processes may also have contributed to the shifts in root traits that occurred during succession. The BSS community has transitioned from being phylogenetically clustered to overdispersed, while exhibiting a concomitant dispersion in aboveground functional traits (Li et al. 2015). Root traits are known to covary with phylogeny across the plant kingdom (Kong et al. 2014, Valverde-Barrantes et al. 2017, Ma et al. 2018); however, in our data set, only SRL showed phylogenetic signal (data not shown). Thus, it is possible that root traits diverged as succession proceeded, likely as a result of

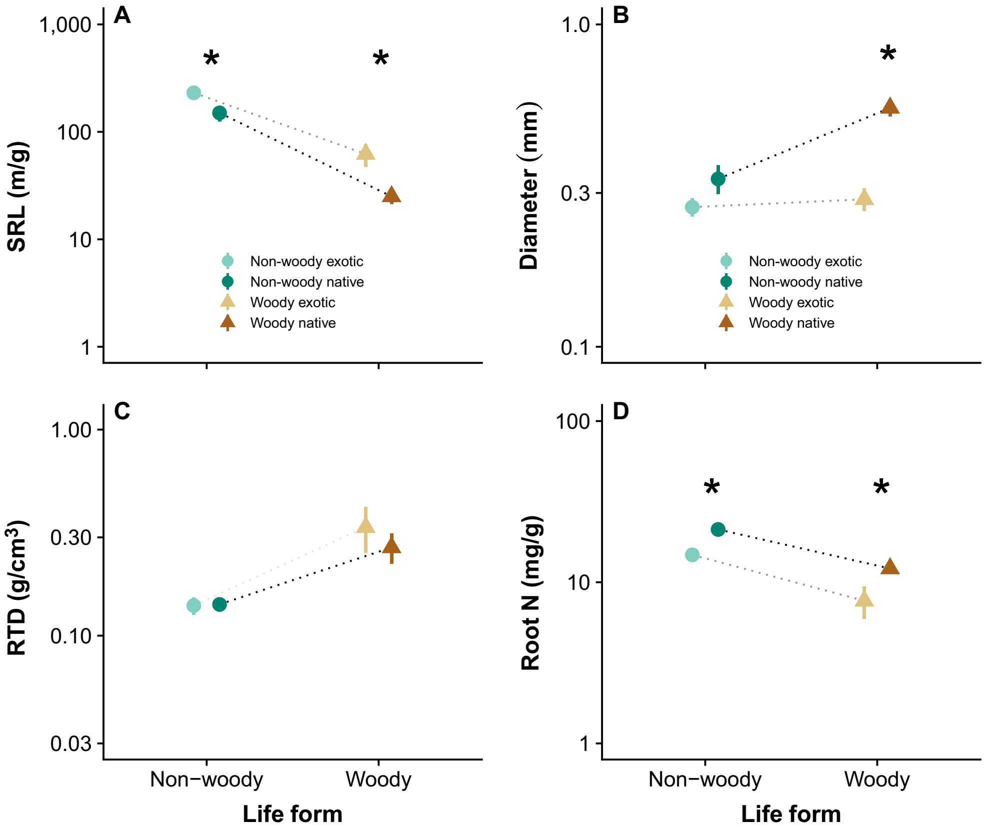

FIG. 2. Trait values (mean ± SE) by life form and species origin. Means differed by life form for all traits (Table 2); asterisks (*) denote significant differences ($P \leq 0.05$) between native and exotic species within forms. Symbols in all panels are as indicated in panels a and b. Note that all *y*-axes are shown on log scales. See Fig. 1 for abbreviations.

ecological processes (e.g., niche complementarity or symmetric competition belowground) or covariation among belowground and aboveground traits. Such processes would have yielded increasing root trait heterogeneity through the course of succession regardless of shifts in mean trait values. Moreover, phylogenetic divergence in the BSS arose because successfully colonizing species became increasingly dissimilar from residents rather than similar species competitively displacing each other more frequently later in succession (Li et al. 2015). It is therefore plausible that increasing niche complementarity belowground mitigated the intensity of competition for soil resources, especially in later successional communities.

One of the primary compositional changes in old-field succession to forest is a transition in dominance from herbaceous to woody species. Woody and non-woody species differ fundamentally in their resource allocation strategies and thus differ in the expression of many leaf and root traits (Laughlin et al. 2010, Pierce et al. 2013, Freschet et al. 2017, Valverde-Barrantes et al. 2017). For this reason, the vast majority of plant trait studies focus on either herbaceous or woody species. In comparing the two groups, we found that the roots of woody and herbaceous species differed markedly in tissue construction (i.e., have larger diameter and RTD but lower SRL and N), with woody species having the more resource conservative strategy. The observation that life form essentially reflects a dichotomous version of the successional gradient in root traits is therefore consistent with expectations. Moreover, similar results were recently found in a study of successional transitions from herbaceous to woody vegetation in Mediterranean roadside communities (Erktan et al. 2018).

The root trait shifts we observed may not simply be a response to changing abiotic and biotic conditions belowground, but may themselves alter rhizosphere microbial communities and nutrient cycling processes during succession. The thinner roots with lower RTD and higher SRL observed in early successional species are often related to shorter root lifespan and faster turnover (Tjoelker et al. 2005, McCormack et al. 2012). Likewise, the more acquisitive roots of herbaceous species have faster decomposition rates (Silver and Miya 2001; C. R. See et al., *accepted*). The predominance of such traits early in succession may therefore contribute greater amounts of labile root litter with a lower C:N ratio, bolstering microbial activity and thus driving soil

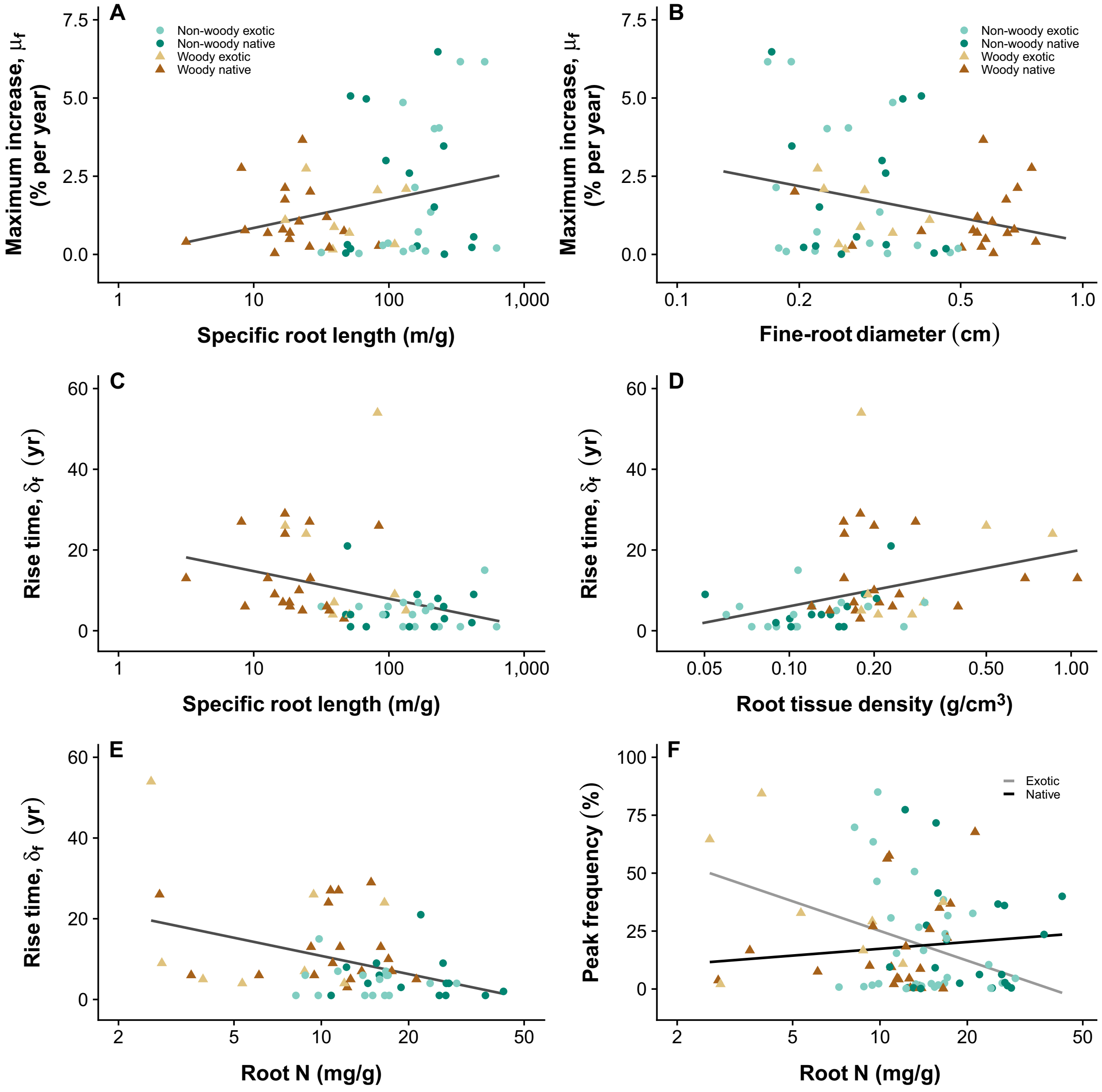

FIG. 3. Relationships between fine-root traits and metrics of species dynamics; each point represents a species. Shown are significant relationships for metrics calculated from plot frequency (Table 3); lines are separated by species origin only if the Trait × Origin interaction was significant. Additional relationships were identified for δ_c and were similar to those depicted (Appendix S1: Fig. S4). Symbol color and shape denote plant form while saturation denotes origin; symbols in all panels are as indicated in panel a. Note that all *x*-axes are shown on log scales. Variables are μ_f, maximum rate of frequency increase; δ_f, time spanning the onset of the species' rise in frequency until μ was achieved; see Fig. 1 for other abbreviations.

fertility and faster nutrient cycling. In contrast, the transition to longer-lived, more recalcitrant tissues could act as a positive feedback in the opposite direction, further slowing nutrient cycling and reducing soil fertility.

Differences by origin

In many cases, exotic plant species that have become abundant in natural ecosystems have traits enabling them to capture and exploit resources to a greater extent than most native species and are thus well adapted to resource-rich environments (Daehler 2003, Leishman et al. 2007, Caplan and Yeakley 2010). Resource exploitation can also interact with other processes, such as release from pathogens or alteration of soil microbial communities, to facilitate invasion (Ehrenfeld et al. 2005, Blumenthal et al. 2009). Such trait differences were observed here, with the three morphological traits we investigated conforming to expectations. However, root N was consistently higher in natives regardless of life

TABLE 3. Statistical results for models relating metrics of species dynamics to fine-root traits and species origin (native vs. exotic).

	Frequency				Cover			
Species metric and term	η	F	df	P	η	F	df	P
μ								
SRL	0.073	4.087	1,52	0.048				
Diameter	0.082	4.637	1,52	0.036				
δ								
SRL	0.130	7.791	1,52	0.007	0.187	10.834	1,52	0.002
Diameter					0.084	4.334	1,52	0.043
RTD	0.121	7.127	1,52	0.010	0.120	6.388	1,52	0.015
Root N	0.181	11.489	1,80	0.001	0.093	4.826	1,80	0.033
Peak abundance								
Root N × Origin	0.069	5.896	1,80	0.017				

Notes: Only significant model terms are shown; see Appendix S2: Table S6 for complete results. μ, maximum rate of abundance increase; δ, time spanning the onset of the species' rise in abundance until μ was achieved; see Fig. 1 for abbreviations of root traits. η values are proportional to the fraction of variation in the response variables explained by each term.

form, despite greater N concentration traditionally being considered the more acquisitive trait manifestation (Reich 2014). This result may be a consequence of selection processes acting differently in different biogeographic contexts or may relate to aspects of root function not encapsulated by the acquisitive to conservative spectrum (Weemstra et al. 2016). Regardless, it may contribute to the success of exotic invaders in communities like those of the BSS and deserves further investigation.

To a limited extent, the way that root traits varied with successional position diverged between native and exotic species. In native species, root diameter increased with the age of peak frequency as the community shifted from herbaceous dominated to woody dominated. In contrast, exotic species maintained consistently low root diameters throughout the successional sequence. Similar context dependence was seen by Tecco et al. (2010), who found that, while exotic woody plants exhibited significantly more acquisitive traits than natives, herbaceous native and exotic species were equivalent. This result corroborates prior suggestions that a number of exotic understory species have invaded temperate forests by capitalizing on anthropogenically altered soil conditions (Gilliam 2006, Smith et al. 2014, Peltzer et al. 2016, Caplan et al. 2017). However, for most root traits, there was no interaction of species origin with successional position. This suggests that, while the average position of native and exotics in the acquisitive-conservative spectrum differs, the underlying successional trade-offs are, in fact, the same (Leishman et al. 2007) and reflect a form of successional equivalence (McLane et al. 2012).

For the root traits examined here, natives typically exhibited a broader range of trait values than exotics, perhaps constraining the potential for changes in traits with successional position seen within the exotics. While the invasion of exotic species is often considered to be derived from unique or extreme trait values (Tecco et al. 2010, van Kleunen et al. 2010, Caplan et al. 2014, Lee et al. 2017), the successful exotic species in the BSS appear to utilize a subset of the same root trait space occupied by native species rather than any ecologically novel part of that trait space. However, while this study and others identify categorical differences in functional traits between native and exotic plant species, it is important to note that there is substantial variation within each group (Dawson et al. 2012*a*, Flores-Moreno et al. 2013); many native species express acquisitive traits and many exotic species express conservative traits, with broad ranges for each.

Relationships with species dynamics

Evidence that interspecific variation in fine-root traits is associated with species dynamics (our third hypothesis) came from multiple traits and metrics; together they demonstrate that root-trait syndromes are linked to broader interspecific patterns in life history and abundance (Reich 2014). While our metrics of abundance had only modest spatial and temporal resolution, they substantiated the idea that species with more acquisitive root constructions tend to achieve more rapid rates of abundance increase and spread (which we quantified as μ) and require shorter time spans to reach these rates (quantified as δ) than species with more conservative constructions. Notably, there were no cases in which species with low SRL and large root diameters had high μ_f, while species with high SRL and small diameters exhibited a range of μ_f values (Fig. 3a, b). Although our investigation was correlative and focused on old-field to forest successional communities, this finding may suggest that acquisitive fine-root traits are an important component of "fast" life history strategies, but are not sufficient to achieve rapid population-level growth without other factors (e.g., sufficient propagule pressure) also being present.

In the case of peak abundance, the expected relationship was not found. This is likely attributable to the overriding influence of other factors like differences in dispersal (both into and within the community), differential mortality due to pests and pathogens, and niche complementarity. The one relationship our analysis identified, that between root N and peak frequency, differed in direction by species origin. The relationship may partially reflect differences in resource acquisition and growth rates for exotic vs. native species, analogous to what has been found in leaves (Leishman et al. 2007). However, this pattern may be more nuanced than that observed in leaves and may have less to do with root N reflecting differences in growth rates and resource acquisition across native and exotic species than would be expected from studies of aboveground traits (Leishman et al. 2007, Dawson et al. 2012*b*). Although root nitrogen concentration varies across soil fertility gradients (Holdaway et al. 2011) and within communities, plant relative growth rate is often decoupled from root nitrogen concentration (Kramer-Walter et al. 2016, Caplan et al. 2017). The lack of a consistent relationship between root N and demographic parameters between native and exotic species may reflect the differential selective forces that act on each group (Müller-Schärer et al. 2004, Hawkes 2007), or even some members of each group, likely weakening any global relationship across species.

Looking forward

One of the primary challenges to fully integrating root traits into plant community ecology is the paucity of data. Despite restricting our analysis to only the four most common traits contained in FRED (of >100), we were able to include just 27% of the 311 species in the BSS data set. While gap-filling allowed us to take maximal advantage of the available data, this approach entails some loss of specificity and cannot be used when trait data cover very few species. Given data limitations, our results and conclusions may be biased toward patterns exhibited by abundant and aggressive species, an issue that may become avoidable once root trait data are available for more species. Greater data availability may also help future studies identify meaningful linkages among belowground strategies, plant performance, and species dynamics that we were unable to detect (Wang et al. 2018). Given that resource uptake by roots can be optimized in multiple ways (Weemstra et al. 2016), far more information on root traits is needed to capture the full range of root foraging strategies and constrain their perceived relationship with species dynamics. For example, having more information on associations with mycorrhizal fungi, fine-root architecture, fine-root life span, and phenology should enable future studies to more fully define strategies of resource allocation and acquisition (Bouda and Saiers 2017, Li et al. 2017, Liese et al. 2017, McCormack et al. 2017). Moreover, the majority of currently available data pertain to fine roots pooled as all roots <2 mm, which mixes distal, absorptive roots that generally lack secondary development with roots primarily involved in resource transport; this muddies the functional application of root trait information. Focusing trait data collection on root order would allow for better functional resolution and likely yield stronger relationships with species dynamics. Furthermore, combining data on fine-root traits with those describing aboveground and whole-plant characteristics (e.g., seed size, leaf lifespan, and clonal reproductive capacity) would allow for a more holistic exploration of linkages between traits and species dynamics. Finally, systematic surveys within diverse communities are needed to form a more comprehensive view of the importance of root traits, particularly in combination with aboveground and whole-plant traits.

Despite these challenges, this study identifies linkages between fine-root traits and species dynamics. Future work marshalling growing trait data sets and extending our hypotheses into other plant communities will undoubtedly expand our understanding of functional connections between belowground foraging strategies and plant performance. This knowledge, coupled with an increasing recognition that fine roots and their associated traits contribute to many long-term processes in soil (e.g., nutrient cycling and buildup of stable soil organic matter) will ultimately lead to better predictions of plant community dynamics and ecosystem processes.

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