The role of intraspecific trait variability and soil properties in community assembly during forest secondary succession

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Abstract. Trait-based approaches applied to community assembly have led to a considerable advance in understanding the drivers that underlie community dynamics. However, species respond to environmental conditions based on traits, and the role of intraspecific trait variability (ITV) in community assembly during succession has not been studied in detail. Here, we explored the effects of environmental conditions on plant trait composition and tested the role of ITV on understanding the assembly processes throughout a long-term forest succession on the Loess Plateau of China. Thirty plots were established across six successional stages, and 15 functional traits of 210 species were measured. Rao’s quadratic entropy of each community with and without accounting for ITV was calculated and then compared with random expectation to evaluate the community functional structure. A structural equation model was used to determine the effects of soil abiotic factors on community functional structure. Community functional structure based on multiple traits transitioned from a stochastic pattern in the early community to a significantly overdispersed pattern in the latest climax community, mainly driven by the increasing niche differentiation of plant height and seed mass. In contrast, community functional structure for most chemical and structure traits showed a neutral but increasing clustering pattern throughout succession. We found that consideration of intraspecific variability did not result in the misreading of the assembly process along a successional gradient; consideration of intraspecific variability only increased the divergence of traits for the latest climax community. Soil NH4-N was an especially important factor that influenced community functional structure and ITV during succession. Our results suggest a change in the dominant assembly mechanism from stochastic to deterministic processes and a strong environmental modification that drives community assembly during a long-term forest succession. Ignoring ITV (except for plant height) may be acceptable in understanding community assembly along a local secondary forest succession in a semiarid ecosystem, such as the Loess Plateau.

Key words: functional traits; intraspecific variation; Loess Plateau; soil properties; structural equation modeling; succession.

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INTRODUCTION

Community ecology aims to understand the processes that shape the structure and composition of communities (Thorn et al. 2016). Functional traits are morphological, physiological, and phenological characteristics of individual organisms that influence fitness and responses to and effects on
the environment (Violle et al. 2007). From a trait-based perspective, a community may be characterized by the distribution of functional traits of the individuals that comprise it (Ackerly and Cornwell 2007). Because of the direct links between traits and the functioning of organisms, trait distributions offer powerful insights into how communities are assembled and how they influence ecosystem processes (HilleRisLambers et al. 2012, Laughlin 2014, Kunstler et al. 2016, Loranger et al. 2016). The effects of traits on community assembly are increasingly understood for specific environmental conditions, and communities are generally regarded as the result of species-sorting processes through deterministic or stochastic processes or by a combination of both (Lohbeck et al. 2014, Kraft et al. 2015, Mären et al. 2017). Deterministic processes have focused on two selective processes: environmental filtering and niche differentiation (Cornwell et al. 2006). Environmental filtering may be viewed as a form of stabilization or directional selection in which the abiotic environment selects for specific trait values, leading to trait convergence within habitats (Lebrija-Trejos et al. 2010, Baraloto et al. 2012). Of course, based on contemporary coexistence theory (Mayfield and Levine 2010, HilleRisLambers et al. 2012, Adler et al. 2013), large fitness differences and competitive exclusion can also lead to trait clustering. Niche differentiation may be viewed as a form of density-dependent selection in which competition and other biotic interactions select against trait values too similar to those of neighbors (Stubbs and Wilson 2004). Stochastic processes would play a dominant role if community assembly was primarily influenced by random dispersal and stochasticity in demographic processes (Zhang et al. 2015, Mären et al. 2017).

A successional series can be viewed as community assembly in progress (Bruehlheide et al. 2011) and has served as a lens for understanding how ecological communities are assembled (Prach and Walker 2011, Lohbeck et al. 2014, Li et al. 2015). Some important studies have tested the changes in the community assembly process during grassland and forest succession using the trait-based method and found that trait-mediated abiotic filtering appears to play an important role in the early stages of succession, whereas the relative importance of niche differentiation appears to increase toward the later successional stages (Purschke et al. 2013, Lohbeck et al. 2014, Li et al. 2015). Nonetheless, studies in relatively severe habitats with cold, dry, or disturbed conditions found contrast changes in the assembly process during succession (Bhaskar et al. 2014, Letten et al. 2014, Zhang et al. 2015, Muscarella et al. 2016). Few studies have focused more on succession as an outcome of stochastic processes and individualistic responses of species to their environment (Mären et al. 2017). Therefore, the differences in assembly processes may be due to different species-level and community-level responses of functional traits to specific environmental gradients during succession because the individual response of a particular species or functional group to changes in resource availability strongly depends on its respective relationship to the affected resource (Adler et al. 2011). Changes in environmental conditions during succession may alter the strength and selectivity of environmental filtering and niche differentiation over time (Bernard-Verdier et al. 2012, Laliberté et al. 2014). Especially for secondary community succession, community species compositions are sensitive to different disturbance types and disturbance intensities (Helmus et al. 2010). Therefore, studying the changes in the assembly process and its response to changes of environmental conditions during succession in different ecosystems allows a better understanding of community assembly.

In addition, although the processes involved in community assembly operate at the level of individual organisms, community assembly processes are traditionally inferred from the mean trait values of fixed species (Chalmendrier et al. 2017). However, traits are not fixed within species. Intraspecific variation due to genetic variation and phenotypic plasticity may strongly contribute to community-level trait variation along gradients (Hulshof and Swenson 2010, Jung et al. 2010, Messier et al. 2010, Leps et al. 2011). Genetic variation and phenotypic plasticity allow the trait values of species to vary among sites in response to environmental filters and interactions with neighboring species (Siefert et al. 2015). These intraspecific shifts in trait values may reinforce interspecific patterns of trait convergence and even spacing, which results in stronger signals of environmental filtering and
niche differentiation when site-specific traits are measured and used rather than fixed mean trait values (Jung et al. 2010, Siefert 2012). Accounting for individual-level variation may therefore be necessary to detect nonrandom community assembly processes (Paine et al. 2011, Violle et al. 2012). Recent studies have shown that intraspecific trait variability (ITV) can significantly affect patterns of community functional diversity of temperate forests (Albert et al. 2012, Bhaskar et al. 2014, Spasojevic et al. 2016) and multispecies community dynamics and robustness (Siefert et al. 2015, Barabás and D’Andrea 2016). However, ITV has yet to be considered in secondary forest successional systems, although it may be particularly important because many common species could occur at different successional stages (Navas et al. 2003) and the variation of environmental conditions during succession may increase the magnitude of ITV at the local scale.

The Loess Plateau in northern China is a semiarid ecosystem that is well known for its deep loess and severe soil water depletion (Wang et al. 2008). The majority of the plant communities on this plateau are currently in the successional transition from abandoned agricultural land to a forest climax community, which reflects anthropogenic disturbances at different time points since the 1860s (Zhu 1993, Chai et al. 2016). A long-term forest succession beginning with abandoned land represents an opportunity to study the entire secondary forest succession under similar starting conditions (Zhang et al. 2015). Previous studies of community succession have rarely been undertaken in a geographic landscape comparable to the Loess Plateau.

In this study, we explored the community assembly based on functional traits over a long-term (approximately 150 yr) arable-to-climax forest succession on the Loess Plateau. We addressed the following questions: (1) Is there a changing contribution of stochastic and deterministic processes in community assembly over a long-term forest succession in the Loess Plateau? We hypothesized that successional dynamics in plant community assembly results from both deterministic and stochastic ecological processes and that their relative importance varies over the successional sequence. (2) Can accounting for intraspecific trait variation affect the testing of community assembly processes over succession? We expect that the effects of ITV on tests of community assembly will be significant in later successional communities in which coexisting species require stronger niche differentiation to cope with increasing competition. (3) In what ways do soil properties affect community functional structure? We expect that the functional community-level responses to changes in resource availability during succession strongly depend on community relationships with the affected resource and that there will be some key abiotic factors that modulate the assembly process during succession.

**Materials and Methods**

**Study site**

This study was performed in the Ziwuling region (35°09′–35°40′ N, 108°47′–108°57′ E), which is located in the middle of the Loess Plateau, Shaanxi, China. The climate is a semiarid, temperate, continental monsoon climate, with generally frequent heavy rainfall events in the summer (Zhu 1993). The mean annual precipitation is 550–650 mm, and the mean annual temperature is approximately 9–11°C. The elevation is from 1100 to 1150 m. Population migration and grain-for-green have led to different levels of restoration of the natural vegetation since the 1860s (Zhu 1993; Fig. 1). The study area (approximately 12 × 15 km) comprises a complex vegetation mixture of forest, shrub, and meadow. Large areas of these communities are now at different stages of forest succession (Zhu 1993; Fig. 1). All community fragments in the present-day landscape were classified according to their successional age, with the help of local chronicles and previous surveys (Zhu 1993, Chai et al. 2015), and were assigned to one of six successional stages (Fig. 1).

Thirty permanently marked plots (five plots per stage) were established in the study area between June and September 2011 to investigate vegetation dynamics following abandonment. The distance between any two plots at the same stage was more than 1 km to include different community types and avoid spatial autocorrelation in variables and pseudo-replications (Conti and Díaz 2013). The plot size was 20 × 20 m. Specifically, our previous survey and study
Fig. 1. (A) Land-cover map of the study area on the Loess Plateau in 2015 and the plot distribution (based on MODIS-NDVI, normalized difference vegetation index). (B) Successional model of the community following abandoned agricultural fields on the Loess Plateau of China (Chai et al. 2019). S1–S6 represent 1–4, 4–8, 8–15, 15–50, 50–100, and 100–150 yr after abandonment, respectively.
ensured that all the plots had the same agricul-
tural history and are now on a similar trajectory
toward climax forest under natural conditions
(Chai et al. 2015). Annuals dominated stage one
(1–4 yr), and the herbaceous perennials *Artemisia
gmelinii* and *Artemisia lavandulaefolia* (Asteraceae)
dominated stage two (4–8 yr). Perennial grass
(Poaceae) dominated stage three (8–15 yr), and
stage four (15–50 yr) was a shrub community. In
the fifth stage (50–100 yr), pioneer tree species
became the dominant growth form. Finally, spe-
cies of the genus *Quercus* dominated the climax
forest stage (100–150 yr). The plots were sam-
ped in 2014, all vascular species within each plot
were identified, and the abundance, coverage,
height, and life form (woody vs. herbaceous) of
the species were documented.

**Trait selection and measurements**

Leaves, stems, and roots each perform critical
functions that together modulate plant survival,
growth, and reproduction (Fortunel and Baraloto
2012, Götzenberger et al. 2012). Here, we
selected 15 plant functional traits from different
organs to explore community assembly (Table 1).
These traits were chosen to represent multi-organ
functions of plants associated with resource use,
dispersal ability, competitive ability, water
balance, and structural defense (Table 1; McGill
et al. 2006, Navas et al. 2010, Laughlin 2014).
Overall, we collected traits of 2856 individuals
from 210 species for analysis. To assess
intraspecific trait variation, all the functional
traits were measured for five or more individuals
of most species within each plot, and the mea-
surements generally followed the protocols of
Cornelissen et al. (2003). Fifteen rare species
(number of individuals <5 in the study area)
were not sampled. The number of individuals
sampled per species is proportional to relative
species coverage, as determined by visual esti-
mation of percent cover following the protocol of
Peet et al. (1998).

**Morphology and structure traits**

For the woody species, completely developed
sun-exposed leaves were randomly sampled
from five healthy branches at a rate of approximately
10–20 leaves per individual. The stem and root on the same individual were sampled;
roots were sampled by excavating the first 20–
30 cm of the soil depth near the plant basal stem.
For the herbaceous species, leaves, stems, and
roots were sampled from five random
0.5 × 0.5 m quadrats within each plot. The fresh
mass ($M_w$) of each leaf, stem, and root was

| Traits | Abbr. | Units | Strategy |
|--------|-------|-------|----------|
| Leaf traits | | | |
| Leaf nitrogen content | LNC | mg/g | Resource capture |
| Leaf carbon content | LCC | mg/g | Resource capture and defense |
| Leaf phosphorus content | LPC | mg/g | Resource capture |
| Leaf N:P ratio | N:P | Ratio | Resource capture |
| Leaf dry mass content | LDMC | mg/g | Leaf structure/water balance |
| Specific leaf area | SLA | m²/kg | Resource capture |
| Stem traits | | | |
| Stem nitrogen content | SNC | mg/g | Resource capture |
| Stem carbon content | SCC | mg/g | Resource capture and defense |
| Stem-specific density | SSD | g/cm³ | Stem structure |
| Stem dry mass content | SDMC | mg/g | Stem structure/water balance |
| Root traits | | | |
| Root nitrogen content | RNC | mg/g | Resource capture |
| Root carbon content | RCC | mg/g | Resource capture and defense |
| Root dry mass content | RDMC | mg/g | Root structure/water balance |
| Seed trait | | | |
| Seed mass | SM | g per 1000 seeds | Dispersal ability |
| Plant trait | | | |
| Plant height | Height | m | Light competitive |
immediately measured with an SE202F electronic balance (Ohaus, Parsippany, New Jersey, USA). An image of each fresh leaf surface was taken with a digital camera, and the leaf surface area (LA) was measured with Motic Images Plus 2.0 (Motic China Group, Xiamen, China) software, except for the leaf area of Pinus tabuliformis, which was estimated following the method of Yan et al. (2006). All samples were placed in a drying oven for 72 h at 80°C to determine the dry mass (MD). The specific leaf area (SLA) was calculated as the ratio of leaf area to dry mass (cm²/g). The dry matter content of the leaf, stem, and root was calculated as MD/Mw. The stem-specific density (SSD) was calculated as the dry mass divided by the stem fresh volume (based on the Archimedes principle, measuring the volume of water displaced by immersion of the stem).

**Stoichiometry traits**

The carbon and nitrogen concentrations of the leaves, stems, and roots were determined with an elemental analyzer (Euro Vector EA3000, Milan, Italy). The total leaf P concentration was determined using the ammonium molybdate spectrophotometric method (Bowman 1988).

**Plant height and seed traits**

Vegetative plant height was measured as the distance between the top of the photosynthetic tissues of each individual and the soil surface. The seed mass data (dry seed mass per 1000 seeds, mg) were assembled by field collections for the majority of species. Because seed mass was thought to be less plastic (Violle et al. 2009), we used the species mean value as the estimate.

**Chemical properties of the soil**

We took eight 3 cm² × 20 cm deep soil cores around each plot and combined them to form a composite sample for each plot that we analyzed for soil properties. A total of five soil properties were assessed, including pH, ammonium nitrogen (NH₄-N), nitrite nitrogen (NO₃-N), phosphate phosphorus (PO₄-P), and soil water content. Soil pH was measured by using a pH electrode (PHS-3C; Shanghai REX Instrument Factory, Shanghai, China). The soil water content was calculated as the ratio of the soil dry mass to the fresh mass (g/g). The other three properties were analyzed using a high-performance microflow analyzer (QuAAtro; SEAL Analytical GmbH, Norderstedt, Germany).

**Analysis: community species composition**

We used Adonis statistical tests to determine whether there were significant differences of community species composition between successional stages. One-way ANOVA was used to compare the changes in species richness among successional stages. A classical canonical correspondence analysis (CCA) was used to investigate the effects of soil properties on community compositions, and the Monte Carlo permutation was used to examine the significance of these effects. Plant community data consisted of the relative abundance of 210 species.

**Analysis: community functional structure**

Rao’s quadratic entropy, calculated here as the mean functional distance between individuals, was calculated to evaluate the community functional diversity (Eq. 1; De Bello et al. 2009, Chalmandrier et al. 2017). First, each functional trait was centered and scaled, and pairwise functional distances between individuals were then calculated by Euclidean distance. Then, we calculated the functional diversity of each community with and without accounting for ITV. To account for ITV, the functional distance matrix was created with all sampled individuals within a given plot. To avoid accounting for ITV, we replaced each individual trait value by fixed species mean trait values (average trait values of all individuals of a given species sampled throughout the study site) before calculating the functional distance matrix as described above. Since traits may represent different niche axes (Spasojevic and Suding 2012), we thus repeated the same analysis described above based on both single traits and multiple traits.

\[
Rao = \left[1 - \frac{1}{N^2} \sum_{k=1}^{N} \sum_{l=1}^{N} d_{kl} \right]^{-1}
\]

where N is the number of individuals in the community, and \(d_{kl}\) is the Euclidean functional distance between individual k and l.

Null models were used to detect or infer assembly processes, such as deterministic
processes and stochastic processes or environmental filtering and niche differentiation, by comparing the functional diversity of observed and randomly assembled communities (Ricotta and Moretti 2011). Specifically, null distributions were generated by randomly assigning, without replacement, all individuals within each plot from all sampled individuals in the landscape to each of the 30 plots. Each null model was run 10,000 times. The standardized effect sizes (SESs) of the Rao values were calculated according to Eq. 2 and were used as an estimation of functional structure. Positive SES values indicate trait divergence, whereas negative values indicate trait convergence. Standardized effect size values greater than 1.96 or less than −1.96 indicate that the observed functional diversity is significantly higher or lower than expected, respectively. The differences in the SES of Rao values between with-ITV and without-ITV cases were assessed by two-tailed t tests. The differences in the SES of Rao values across the six successional stages were examined by one-way ANOVA.

\[
\text{SES}_{\text{Metric}} = \frac{\text{Metric}_{\text{observed}} - \text{Metric}_{\text{randomized}}}{\text{sdMetric}_{\text{randomized}}}
\]

where \(\text{Metric}_{\text{observed}}\) is the observed value, \(\text{Metric}_{\text{randomized}}\) is the mean of the simulated values, and \(\text{sdMetric}_{\text{randomized}}\) is the standard deviation of the simulated values.

**Analysis: variance decomposition**

Linear mixed models (Bolker et al. 2009, Albert et al. 2010) were used to determine the percentage of variability attributed to each level (interspecific, intraspecific between successional stages and intraspecific within successional stages). The general structure of our analyses involved each of the plant trait response variables being modeled as a function of the fixed effect succession stages, with species specified as a random effect. Models were calibrated for each functional trait using individual trait measurements and included either no fixed effects (written as fixed ~ 1, \(m_0\)) or a succession stage fixed effect (fixed ~ succession stage, \(m_1\)) and a random intercept species effect (random ~ 1|species). Estimated standard deviations at the succession stage level (\(r\)) were used to determine the percentage of variability attributed to each level. As species were represented as a random effect, the between-species parts of variance were determined as the ratio between \(r^2\) and total variance. As successional stages were represented as a fixed effect, we calculated a measure of explained variation based on the variances at stage level for the different models following (Xu 2003):

\[
R^2 = 1 - (\delta_{m1})^2/(\delta_{m0})^2,
\]

where \(\delta_{m1}\) and \(\delta_{m0}\) are the estimated error standard deviations at stage level estimated under models \(m_1\) and \(m_0\), respectively. Variances were estimated by maximizing the restricted log-likelihood (REML).

**Analysis: structural equation modeling**

Structural equation modeling (SEM) was used to determine the relative importance of the effects of soil resource factors on community functional structure. SEM is an extension of multiple regression analysis that allows the testing of direct and indirect effects (Vile et al. 2006).

We first developed a general conceptual model that represents how long-term soil and ecosystem development can drive changes in functional structure (Fig. 2). Long-term soil and ecosystem development (here represented by “succession stage”) can lead to changes in soil resource factors that have been emphasized as key drivers of community functional structure (Bernard-Verdier et al. 2012). In addition, soil development leads to changes in abiotic conditions, such as fluctuations in soil water concentrations and pH, which can also affect the local soil resource factors (Laliberté et al. 2013). Finally, the soil conditions and single-trait functional structure can lead to the stage-specific multi-trait functional structure. Maximum likelihood solution procedures were used for all data sets for consistency. A slightly changing slope angle may affect community- and species-level values in traits (Bouchet et al. 2017). Pre-analyses showed that slope angle only had a small variation among plots and did not show relationships with community functional structures (Appendix S1: Table S1), and they were thus not taken into account in this analyses. When analyzing experimental data under an SEM framework, ordinal variables can be dealt with in several ways (Grace 2006). We ranked the successional stage variable as a continuous variable from 1 to 6. Multicollinearity
among independent variables in the final model was tested with principal component analysis and by determining the variance inflation factor associated with each independent variable (Kutner and Nachtsheim 2004). Only those traits found to significantly contribute to the whole functional structure or to significantly respond to specific soil properties were retained in the models. All coefficients shown in the results were standardized. Two models (with and without ITV) were independently developed to allow a comparison between the two sets of results.

Standardized major axis (SMA) tests (Freschet et al. 2012) were then performed to compare how the relationships of community functional structures vs. environmental factors varied when the functional structures were created with and without ITV. When comparing regressions, differences can occur in elevation (y-intercept) and/or slope (regression slope).

All the statistical analyses were performed by the R package ade4 (Dray and Dufour 2007), picante (Kembel et al. 2010), and vegan in R version 3.10 (R Development Core Team 2014) and the SMATR software (version 2.0, Macquarie University, Sydney, Australia).

**RESULTS**

*Community species composition across six successional stages*

Community species richness significantly increased during succession, and most species were distributed in more than two succession stages (Appendix S1: Fig. S1). The CCAs and Adonis tests showed that plant community composition had a significant change during forest secondary succession (Fig. 3, Table 2). Generally, the communities of earlier stages (S1–S3) clustered together, and those of later stages (S4–S6) clustered together (Fig. 3). All soil abiotic properties (pH, NH$_4$-N, NO$_3$-N, total N, total C, and PO$_4$-P) were significantly associated with the plant community composition (Fig. 3; Appendix S1: Table S2).
Community functional diversity and structure during succession and the role of intraspecific trait variability

Community functional diversity (Rao values) based on multiple traits significantly increased with forest succession, and comparative analyses with random communities showed that functional structure transitioned from a stochastic pattern in the early stages to a significant overdispersion in the latest stage (Fig. 4). Functional structure that included ITV was significantly different from functional structure that excluded ITV only in the latest succession stage (Fig. 4B).

Single-trait analyses showed that the SES of Rao for most traits, except for height and seed mass, showed a stochastic pattern (−1.96 < SES < 1.96) over succession (Fig. 5), whereas they were different among succession stages (Appendix S1: Fig. S2). Functional structures of plant C, N, P, and SLA were more overdispersed at stage 1 than in later succession stages (S2–S6). In contrast, the functional structures for seed mass and plant height were more overdispersed at the latest stage than at early succession stages (S1–S5; Appendix S1: Fig. S2). The inclusion of ITV generally influenced the estimation of community functional diversity and structure at the latest.

Fig. 3. Canonical correspondence analysis showing the effects of soil abiotic properties on the community species composition across the six successional stages (S1–S6 represent 1–4, 4–8, 8–15, 15–50, 50–100, and 100–150 yr after abandonment, respectively). Soil properties: pH, water content (soil water), available phosphorus (PO4-P), ammonium nitrogen (NH4-N), and nitrate nitrogen (NO3-N). F-value of Monte Carlo permutation testing for the effect of soil properties is provided, with the level of significance set at $P < 0.05$. 

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successional stage, except for SSD and leaf N:P (Fig. 5), and only worked for a few traits (stem carbon content, stem nitrogen content [SNC], and root nitrogen content) at other stages (S1–S5). Functional diversity based on single traits showed a pattern similar to that of functional structure (Appendix S1: Figs. S3, S4).

### Variance decomposition

Single-trait analyses revealed a partition at approximately 67% vs. 33% for interspecific vs. intraspecific variability (Fig. 6), respectively. On average, ITV within succession stages accounted for 8% of total trait variance and ITV among succession stages accounted for 27% of total trait variance.

### The roles of soil properties in mediating functional structure and ITV

Eight and five traits were retained in the two models (with and without ITV), respectively (Fig. 7A, B). The resulting SEM was well supported by the data (Fig. 7A, $\chi^2 = 42.6, P = 0.17$; Fig. 7B, $\chi^2 = 49.7, P = 0.19$), and none of the independence claims implied by the model were statistically significant ($P > 0.05$), which suggests that all the important relationships were specified in the model.

Long-term community succession led to strong increases in soil NH$_4$-N and declines in soil NO$_3$-N and pH, and pH showed significant negative effects on soil NH$_4$-N and positive effects on soil PO$_4$-P. The change in community functional structure of a specific trait depended on its respective relationship to the affected resource either directly or indirectly (Fig. 7A, B). Functional structures based on leaf traits (SLA, Leaf carbon content [LCC], and leaf nitrogen content

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**Table 2. Changes of plant community composition by Adonis tests.**

| Between successional stage | $F$  | $P$  |
|----------------------------|------|------|
| S1 S2                      | 2.05 | 0.10 |
| S1 S3                      | 1.45 | 0.08 |
| S1 S4                      | 3.41 | 0.01 |
| S1 S5                      | 2.88 | 0.00 |
| S1 S6                      | 3.08 | 0.01 |
| S2 S3                      | 1.06 | 0.44 |
| S2 S4                      | 2.29 | 0.01 |
| S2 S5                      | 2.33 | 0.02 |
| S2 S6                      | 2.55 | 0.01 |
| S3 S4                      | 2.21 | 0.01 |
| S3 S5                      | 2.04 | 0.01 |
| S3 S6                      | 2.16 | 0.00 |
| S4 S5                      | 2.30 | 0.01 |
| S4 S6                      | 2.78 | 0.00 |
| S5 S6                      | 1.46 | 0.07 |

Notes: S1–S6 represent 1–4, 4–8, 8–15, 15–50, 50–100, and 100–150 yr after abandonment, respectively. Bold fonts indicate significant difference ($P < 0.05$).

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**Fig. 4.** Changes of community (A) functional diversity (Rao value) and (B) functional structure (standardized effect size [SES] of Rao) based on multiple traits during succession. The functional structures were measured as SESs for Rao values. Standardized effect size $>0$ represents functional divergence, whereas SES $<0$ indicates functional convergence. Each point shows the mean SES values among all plots within each successional stage. Error bars represent standard errors. Asterisks indicate significant differences between metrics with and without intraspecific trait variability (ITV), and plus signs indicate significant differences between metrics and 1.96.
[LNC]) showed similar responses to environmental conditions either with or without ITV (Fig. 7A, B) and were driven by soil water content, pH, and NH₄-N, respectively. NH₄-N was the key environmental variable that especially influenced the functional structure of seed mass (Fig. 7B). Ignoring intraspecific variation mismatched the effects of environmental conditions.
on plant height and overrated the selective stress of successional soil conditions for stem dry mass content (SDMC), SNC, and root dry mass content (RDMC; Fig. 7A, B; Appendix S1: Fig. S5). When ITV was not included, the variation in community functional structure based on multiple traits was explained almost entirely by plant height (Fig. 7A), whereas it was mainly explained by seed mass after accounting for ITV (Fig. 7B). Overall, NH4-N showed the greatest total effects on the community functional structures (Fig. 8A, B).

**Discussion**

**Community assembly process based on fixed species mean traits during forest succession**

Community functional structure based on multiple traits transitioned from an early stochastic pattern to the significant overdispersion of the climax community stage, which indicates the change of the dominant assembly mechanism from stochastic to deterministic processes during the long-term forest secondary succession on the Loess plateau. This does not support a progression from habitat filtering to competitive exclusion as in tropical forest succession (Lohbeck et al. 2014). First, the stochastic pattern of early successional stages may be due to dispersal limitation. In the Loess Plateau, multiple vegetation types were mosaic distributions because of intermediate cuttings at different times. Species composition of the early community was strongly influenced by the surrounding species pool, which is related to spatial distance (dispersal limitation). A previous study even found the similar result that dispersal limitation can limit species distribution in secondary forest succession (Verheyen and Hermy 2002). However, the importance of distance (dispersal limitation) is likely to decrease over time as colonization continues, with the secondary forest maturing and developing. In the meantime, the importance of recruitment limitation related to habitat quality (deterministic factors) increases with succession (Verheyen and Hermy 2002, Carnicer et al. 2014), which results in the increasing differentiation of functional
Fig. 7. Structural equation model showing the direct and indirect pathways through which long-term soil and ecosystem development drives variation in community functional structure. Arrows represent the flow of causality. (A) Model without intraspecific trait variability (ITV). (B) Model with ITV. The models were well supported by our data, (A): $\chi^2 = 42.6$, df = 48, $P = 0.17$; (B): $\chi^2 = 49.7$, df = 56, $P = 0.19$, and none of the independence claims implied by the model were statistically significant at $a = 0.05$. Path coefficients were standardized. Arrow width is proportional to the standardized path coefficient and can be interpreted as the relative importance of each factor. Abbreviations for traits: leaf nitrogen content (LNC), leaf carbon content (LCC), leaf phosphorus content (LPC), leaf dry mass content (LDMC), special leaf area (SLA), leaf N:P (N:P), stem-specific density (SSD), stem dry mass content (SDMC), stem nitrogen content (SNC), stem carbon content (SCC), root dry mass content (RDMC), root nitrogen content (RNC), root carbon content (RCC), seed mass (SM), and plant height (Height).
strategies for species coexistence in the climax community. In addition, other stochastic processes typical to secondary forest ecosystem may also contribute to this pattern (Mären et al. 2017) since colonizers in the early unsaturated communities often include the species that resprout from roots or randomly surviving plants. Of course, the confounding effects of traits may also result in the stochastic patterns of functional structure (Butterfield and Suding 2013) because the selected traits represent multiple ecological strategies and seed mass and plant height showed contrasting functional structure compared with stoichiometry and structure traits at the same succession stage.

Trait overdispersion in late successional communities has been commonly observed in other successional series (Norden et al. 2012, Purschke et al. 2013). Moreover, this pattern is generally attributed to the elimination of functionally similar species caused by competitive interactions (Purschke et al. 2013) or colonization of distantly related species (species turnover; Li et al. 2015). In the present study, single-trait analyses and SEMs revealed that the later assembly pattern was only driven by the overdispersion of seed mass and height at the latest stage. Plant height was used to represent the light competitive ability, resource acquisition, and allocation strategies of species (Swenson et al. 2012, Lasky et al. 2014). Seed mass is commonly associated with the dispersal ability and colonization strategies of species (Cornelissen et al. 2003). Overdispersion of seed mass and plant height for later succession communities is easy to understand and consistent with the successional niche hypothesis (Muscarella et al. 2016) that vertical stratification in a successional climax community creates a more complex light and nutrition environment than in an early community and that coexisting species showed more niche specialization and separation than did species of early successional communities. Our results emphasize that significant overdispersion especially occurs only in the climax forest community rather than in other stages, which indicates a slower increase of niche differentiation during succession in semiarid ecosystems compared with that in tropical ecosystems (Lohbeck et al. 2014). This may be related to the difference of competition intensity

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**Fig. 8.** Total effects of soil conditions on functional structures of different traits; with intraspecific trait variability (ITV) (A) and without ITV (B). Relative importance of different soil factors is represented by standardized path coefficients from the structural equation model. Abbreviations for traits: leaf nitrogen content (LNC), leaf carbon content (LCC), special leaf area (SLA), stem dry mass content (SDMC), root dry mass content (RDMC), root carbon content (RCC), seed mass (SM), and plant height (Height).
between the two ecosystems. Competition intensity in the tropical forest ecosystem is highest during intermediate development stages because of rapidly increasing species diversity (Chanthorn et al. 2017).

Although the functional structures for most traits showed a stochastic ($-1.96 < \text{SES} < 1.96$) pattern (Fig. 5) over the entire succession process, there were significant differences among different succession stages. Functional structures of plant C, N, P, and SLA converged more at later succession stages (S2–S6) than in stage 1. Increasing functional convergence during succession has only been separately found for forest (Bhaskar et al. 2014, Muscarella et al. 2016), scrubland (Letten et al. 2014), or grassland communities (Zhang et al. 2015), and these studies are generally in relatively severe habitats with cold, dry, or disturbed conditions. We confirmed this phenomenon during a long-term forest succession in the semiarid ecosystem. In the Loess Plateau, natural vegetation experienced serious anthropogenic interference and water and soil erosion, which is similar to a fire, before conservation and restoration of vegetation. First, plant C, N P, and SLA are sensitive to soil condition and microhabitat heterogeneity (Richardson et al. 2012, Nikolic et al. 2014), and their functional structure may thus be considered a consequence of increasing environmental filtering throughout succession in the Loess plateau. Second, biotic interactions such as competition may increasingly also work in the convergence of stoichiometric traits in later succession stages because if most species are competitively excluded from the community, the remaining assemblages should show a low value of functional diversity since the common dominant species is present in most plots (Bennett et al. 2013). In the present study, Quercus is the common and dominant genus in the climax and is particularly abundant in late communities, which represents a strong impact of species abundance on late community assemblages. Therefore, competition exclusion and environmental filtering may work together, counteract each other, and then produce stochastic but increasing clustering patterns for stoichiometry and structure traits.

Overall, we determined a novel change from stochastic to deterministic processes during forest succession in a semiarid ecosystem. Species at later succession stages must show differences in trait values for traits related to competition (e.g., seed mass, plant height), which enables reduced interspecific interference and avoids competitive exclusion (Muscarella et al. 2016); however, those species should also show similar values on some other traits related to habitat filtering (e.g., C, N, P, and SLA) to support the same abiotic pressures. In the present study, we did not sample for rare species. This did not affect the estimate of functional structure and diversity because those metrics were calculated by species trait values that were weighted based on relative coverage. Rare species generally have low relative coverage in a community and neglecting rare species in this study thus did not influence the conclusions.

The role of intraspecific trait variability in understanding community assembly during forest succession in a semiarid ecosystem

In contrast, with our hypothesis, although accounting for ITV significantly allowed the detection of niche differentiation at the latest successional stage, including ITV did not significantly influence the direction of change in assembly patterns either for multi-trait or single traits during succession. The SEM results also showed that neglecting ITV did not influence the contribution of traits to the entire functional structure, except for plant height. This is because the contribution of interspecies variability is larger than that of intraspecific variability, approximately 67% vs. 33% for interspecific vs. intraspecific variability, respectively. High interspecies variability is related to the large species turnover between succession stages during long-term forest succession (Fig. 3, Table 2). Indeed, plant species composition undergoes significant changes during forest succession; this rapid change is common in arid and semiarid regions (Lozano et al. 2014). Previous studies proposed that intraspecific variation is negligible at very broad spatial scales that encompass strong environmental gradients and that using species mean trait values to characterize community-level trait patterns is thus acceptable (Albert et al. 2011, Siefert et al. 2014, Lajoie and Vellend 2015). In the case of including wide range successional stages from the annual herb stage to the climax forest stage, we argued that it may be acceptable.
to use species mean value (except for plant height) to study the community assembly of forest secondary succession in a semi-arid ecosystem, even if it does not contain very broad spatial scales.

Although considering ITV did not significantly influence the major assembly process over forest succession, the relative extent of ITV was distinct among different components of variation decomposition. ITV among succession stages was on average higher than that within succession stages. This is in line with previous studies that found that the relative extent of ITV tended to be greater among communities than within a community either at a local scale in the mountain vegetation of the central French Alps (Albert et al. 2010) or at a global scale (LaJoie and Vellend 2015, Siefert et al. 2015). We therefore inferred that replacement of species would change the adaptive strategy of a certain species that existed in different succession stages.

The roles of soil properties in mediating community assembly and ITV

Soil properties are important factors that mediate the variation of plant community traits along environmental gradients (Ordoñez et al. 2009, Cadotte and Tucker 2017). To determine the effects of soil properties on community functional structures, we translated our conceptual causal model into two models (without and with ITV) that could be quantitatively evaluated. Comparing the two models, we found some common information.

First, long-term forest succession led to strong shifts in the local soil abiotic factors (soil NH₄-N, water content, pH, and NO₃-N), which is in line with previous study in the Loess Plateau (Deng et al. 2014). These factors directly or indirectly influenced community functional structure (Fig. 7A, B), and soil NH₄-N was the most important factor that influenced community functional structure. Moreover, this result is robust either with or without ITV, which indicates a strong modification of the nitrogen cycle in driving community assembly during succession in the Loess Plateau. Soil NH₄-N played a positive role in the niche differentiation of seed mass along the succession. A possible interpretation is that soil NH₄-N stocks and the complexity of the light environment increase with forest succession, which confers better survival and more niche space to large-seed species and thus indirectly leads to divergence of seed traits and a later successional community. This mechanism has previously been detected experimentally in Mediterranean shrubland (Walters and Reich 2000), where it was found that interactions among light and available N could influence seed mass and plant growth. However, NH₄-N showed a negative effect on the functional structure of LNC. This is related to the strong N-limited and water-limited conditions on the Loess Plateau (Wang et al. 2008, Chai et al. 2015). The community trait value of leaf N:P was always lower than 16 (Appendix S1: Fig. S6), which confirms this relation. This strong stressful condition may increase with community succession and may force species to develop similar LNC. The effects of soil pH and water content on the functional structures of LCC and SLA during succession were uniform for the two models. This is in line with the results from other grassland successional series (Laliberté et al. 2014, Zirbel et al. 2017). These results support the hypothesis that community functional structure could show distinct patterns caused by the dependence on soil properties (Thorn et al. 2016). We extended this hypothesis in a long forest secondary succession and found the key soil driving factor that influenced community assembly.

Second, compared with the model without ITV, three traits (SDMC, RDMC, and SNC) were removed in the model considering ITV. This suggests that the ITVs of these traits weaken the relationships between functional structure and soil properties. The SMT tests confirmed the differences of relationships based on either slope or elevation (Appendix S1: Fig. S5). However, the functional structures based on leaf traits (SLA, LCC, and LNC) showed very stable response to environmental condition either with or without ITV. These results indicate stronger environmental filtering acting on leaf traits than on stem or root traits along the successional gradient. Theoretically, strong trait coordination exists across traits from different plant organs. For example, LNC is linked to SNC (Freschet et al. 2010) and SLA to SDMC and RDMC (Liu et al. 2010). Nonetheless, under stressful environments, leaf, stem, and root traits could show differences in the intensity of the response to environment conditions.
gradients and could show contrasted intraspecific responses across species, which then weakens the coordination at the community level.

**Conclusions**

By using data of a long-term forest succession, our study tests a deterministic successional pattern in community functional structures and highlights the importance of NH$_4$-N as the key soil factor in the community assembly of the secondary forest succession. The role of ITV in understanding community assembly depends on the environmental axis and traits considered. Consideration of intraspecific variability may not be necessary for most traits (except for plant height) to study community assembly in a semi-arid ecosystem, such as the Loess Plateau. Environmental filtering acting on leaf traits might be especially stronger than that acting on stem or root traits during forest succession in the Loess Plateau. Our findings have important implications for understanding community assembly during forest succession in the semi-arid ecosystem and for more pragmatic matters, such as informing community restoration based on trait-based principles.

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