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What causes greater deviations from predictions of metabolic scaling theory in earlier successional forests?

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ABSTRACT

Metabolic scaling theory (MST) is frequently criticized because its predictions do not match many observations that allometric relationships change with climate and species. Understanding why observations deviate from theory predictions is critical for better forest carbon accounting and management in a rapid warming world. Here we used forest plots across successional and latitudinal gradients to test the predictions that: (1) observed exponents should deviate more from MST predictions at earlier successional stages; (2) the deviations may be related to changes in competition, recruitment limitation and tree size across successional stages and climate gradient. We sampled forest plots (each 1000 m^2) from four successional stages (early to late) in four sites along a latitudinal gradient (42–50°N) in Northeast China, and examined the scaling relationship between tree diameter and height (*D-H*) and plot-level tree size distribution (*D-N* scaling). We related the scaling exponents for each plot to successional stage, climate, local topographic factors, and proxies for tree size, light competition and recruitment limitation. We used mixed-effect structural equation model to examine the major factors causing the deviations from MST predictions. The results showed that both *D-H* and *D-N* scaling exponents conformed to MST predictions in late-successional forests, but *D-H* exponent deceased while *D-N* exponent increased regularly towards later-successional stages. Both exponents were little correlated with climate and local topographic factors, but were significantly correlated to tree size, and proxies for competition (stem density) and recruitment limitation (skewness of tree size distribution). *D-H* scaling was mainly affected by stem density and successional stage, while *D-N* scaling mainly affected by skewness and succession. Both scaling relationships were not significantly affected by tree size, and were indirectly influenced by climate through stem density or skewness. Our results provide clear evidence that MST predictions are only supported in the late successional forests, while forests at an earlier successional stage reveal greater deviations. These deviations may be caused by processes not considered in MST, including light competition, demography dynamics and successional status. Future MST need to incorporate these ecological processes to better predict the allometries for disturbed forests, which are widespread across the world and have important roles in carbon sequestration.

1. Introduction

Allometric relationships are basic tools for estimating forest carbon pools and sinks (e.g. Chave et al., 2014). Understanding whether there is a general allometry law across forest types and environmental gradients is critical for forest carbon accounting and management in a rapid warming world. Consequently, allometry has long been a focus in ecology and many hypotheses have been proposed. Among which, the metabolic scaling theory (MST) is based on some basic biophysical constraints (West et al., 1997, 1999), and have provided testable predictions for many scaling relationships from organ to ecosystem scales (Brown et al., 2004; Enquist et al., 2007b, 2009).

MST has widely received attention because of both its theoretical importance, and its important potential in forest carbon accounting (e.g. Enquist and Niklas, 2001; Brown et al., 2004; Chave et al., 2014). However, MST has also been controversial since it was proposed. A major reason it is criticized is because its earlier model for trees (widely known as WBE) predicts a specific exponent for each scaling relationship, around which species from different taxa and environment should cluster (West et al., 1997; Enquist and Niklas, 2001). However, many

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studies found that allometry exponent not only differ among forest types (species), but also change regularly with climate and tree size (Muller-Landau et al., 2006; Wang et al., 2006; Lines et al., 2012; Duncanson et al., 2015; Hulshof et al., 2015; Poorter et al., 2015), and thus do not match the exponent predicted by MST. While these criticisms may not be enough to reject MST, it is also evident that MST need to be improved, and understanding why observations deviate from MST predictions is critical for this purpose (Rüger and Condit, 2012; Duncanson et al., 2015).

Recently, Duncanson et al. (2015) proposed an explanation for why observed scaling exponents deviated from MST predictions. They noted that MST is based on several simplifying assumptions including: (1) forests are assumed to be in approximate steady state with respect to resources and demographics, which also means that there's no recruitment limitation and external disturbance. (2) Trees grow and fill up all the available space. Clearly, these assumptions can only be met in late successional forests. In forests that have suffered disturbance, where the steady-state conditions are violated, allometry exponents should deviate from MST predictions. Duncanson et al. (2015) examined the relationship between tree diameter and height (*D-H* scaling hereafter), and plot-level tree size distribution (*D-N* scaling), for plots across the United States. They showed that both scaling exponents were consistent to MST predictions in forests with height > 35 m (assumed to be mature forests), but deviate from MST predictions for forests < 35 m height (assumed to be younger forests).

This hypothesis is interesting, but there are still some points that need further examination. (1) From the hypothesis, it can be further predicted that (Prediction 1): since the assumptions of "steady state" are more violated at earlier stages of forest succession than later ones, allometric exponents should deviate more from MST predictions at an earlier successional stage. Duncanson's hypothesis is valid only when this prediction is supported, and here we used plots from early- to late-successional stages to test it. (2) Duncanson et al. (2015) found that both the *D-H* and *D-N* scaling exponents increased with forest height (when forest height < 35 m). Since shorter forests were assumed to be younger while tall forests assumed to be mature forests, their results seem to suggest that the two exponents would increase from early- to late-successional stages (Prediction 2.1). However, according to recent models of MST, the *D-H* allometric exponent is predicted to decrease with larger plant size (e.g. Enquist et al., 2007a; Niklas and Spatz, 2004). Thus *D-H* scaling should decrease from early- to late-successional forests with increasing tree sizes (Prediction 2.2). We examined which prediction is true.

MST has long been criticized to implicitly assume that allometric exponents are independent of environment and species composition (e.g. Lines et al., 2012; Duncanson et al., 2015). However, actually MST studies have proposed a hypothesis for changes of scaling exponents with climate and species, but has seldom been tested. MST now days predicts that allometric exponents changes continuously with plant size (Niklas and Spatz, 2004; Enquist et al., 2007a; Price et al., 2007). It is well known that tree size changes greatly across climate gradient and species (e.g. Wang et al., 2006; Moles et al., 2009; Lines et al., 2012). It is thus possible that climate and species do not affect scaling exponents directly, but only affects plant size, which in turn lead to changes in allometries (Niklas and Spatz, 2004). In this situation we may still observe a significant correlation of allometric exponents with climate and species, as reported in many studies (see above). Thus, these studies may not necessarily falsify MST. Similarly, tree size also increase markedly during forest succession, and it is also possible that the difference in scaling relationships among successional stages are caused by changes in tree size. Here we tested the prediction that climate and successional stages only affects allometries indirectly via their effects on tree size (Prediction 3). If true, then many observed changes in allometries with climate and forest types can be explained by MST itself, without invoking other mechanisms.

However, if Prediction 3 is not supported, this may suggest that MST need to incorporate more ecological processes. Competition for light has widely been recognized as a key factor affecting tree allometries (e.g. Coomes and Allen, 2007; Lines et al., 2012). Some authors also suggest that recruitment limitation and disturbance have important influence on scaling relationships (Coomes et al., 2003; Duncanson et al., 2015). But these processes are not yet well represented in MST (Price et al., 2007; Enquist et al., 2009). Here we examined whether the deviations from MST predictions can be explained by these factors, which is critical for improving MST. Similar as tree size, competition and recruitment limitation are also markedly influenced by environmental gradients and successional stages. For instance, stem density (closely related to competition) is widely observed to change across climatic gradients (Wang et al., 2006; Fang et al., 2012a) and differ among successional stages. Meanwhile, forest demographic dynamics, including recruitment limitation, are also influenced by environmental gradients (Aiba and Kitayama, 1999; Duncanson et al., 2015). Thus climate and successional stage may also affect scaling exponents via their influence on these biotic factors. However, till now how climate and successional stage interact with tree size, competition and demography in affecting scaling relationships have not been well understood. Many previous studies did not included these mechanisms simultaneously, and generally analyzed their influence with correlative methods (which may not be reliable). Here we use a pathway network that is designed to test the above-mentioned hypotheses related to MST, in order to better understand the major mechanisms affecting *D-H* and *D-N* scaling relationships.

In this study, we sampled forest plots across different successional stages at four sites along a latitudinal gradient in northeast China. We examined *D-H* and *D-N* scaling relationships to answer three questions as follows. (1) To test our Prediction 1 that earlier successional forests will show more deviations from MST predictions, and to examine whether the two scaling exponents increase or decrease towards late successional forests (Prediction 2.1 vs. 2.2). (2) To test the Prediction 3 that geographic variation of scaling exponents can be explained by the change of tree size with climate and successional stages. (3) To examine whether the deviations from MST are related to changes in competition and demography across climate gradient and successional stages, and whether the major modulators of *D-H* and *D-N* scaling are different.

2. Methods

2.1. Study sites and data sampling

To examine the influence of climate and forest succession on scaling relationships we selected four sites (Mt. Changbai, Jiaohe, Wuying and Shengshan) in northeast China (Table 1), which covered a latitudinal gradient from 42.3°N to 49.5°N. As a result of large climate gradient (Table 1), these sites covered most of the latitudinal range of the zonal temperate forests (broadleaf Koran pine mixed forest, BKPF) in northeast China, with the Shengshan site located at the north limit of BKPF. In each site we sampled four typical successional stages of BKPF. (1) Late successional forest, dominated by *Pinus koraiensis*, and mixed with broadleaf species such as *Fraxinus mandschurica*, *Tilia* spp., *Acer* spp. etc. (2) Mid-late successional stage, which were disturbed BKPFs but the disturbances were not enough to turn them into typical secondary forests. (3) Middle successional forest, composed of deciduous broadleaf species including *Quercus mongolica*, *Tilia* spp., *Acer* spp. and *Fraxinus mandschurica*, etc. (4) Early successional forest, dominated by light-demanding species such as *Betula platyphylla* and *Populus davidiana*.

We established three plots (50 × 20 m) as replicates in each forest type by each site, and a total of 48 plots were investigated in the summer of 2012 and 2013. In each plot, we recorded geographic coordinates (latitude, longitude and elevation) and local topographic factors (slope and aspect). For trees with a diameter > 5 cm, we measured diameter at breast height (1.3 m), and tree height was

Table 1
General information for the plots sampled from four successional stages of broadleaf Korean pine mixed forests in four sites across latitude in Northeast China. For each forest type by each site, the mean value (± standard error) of three replicate plots was reported for each stand parameter (e.g. density).

Site	Latitude (°N)	Longitude (°E)	Altitude (m)	Successional Stage	Stem Density (/ha)	Mean Diameter (cm)	Canopy height (m)	Maximum stock Volume (m^3)
Mt. Changbai	42.4	127.9	953	Early	1183 ± 93	15.8 ± 1.2	27.7 ± 1.5	1.7 ± 0.3
				Middle	503 ± 131	19.9 ± 5.4	25.3 ± 5.5	5.5 ± 3.0
				Mid-late	453 ± 103	26.9 ± 1.3	32.4 ± 3.1	6.8 ± 2.6
				Late	650 ± 35	24.0 ± 1.0	28.1 ± 5.3	6.8 ± 2.8
Jiaohe	44.0	127.7	473	Early	997 ± 87	16.2 ± 0.9	29.8 ± 1.1	1.9 ± 0.1
				Middle	747 ± 136	20.7 ± 1.5	26.2 ± 1.2	2.5 ± 0.5
				Mid-late	780 ± 123	18.8 ± 1.0	25.4 ± 2.1	3.4 ± 1.7
				Late	533 ± 35	24.7 ± 2.4	25.5 ± 0.7	3.8 ± 0.8
Wuying	48.1	129.1	362	Early	1447 ± 479	13.9 ± 2.8	22.6 ± 0.7	2.0 ± 1.7
				Middle	827 ± 91	16.9 ± 0.7	24.5 ± 0.9	1.8 ± 0.2
				Mid-late	797 ± 51	16.4 ± 2.9	27.3 ± 5.1	7.0 ± 4.1
				Late	730 ± 125	22.7 ± 2.8	30.0 ± 1.3	6.5 ± 2.7
Shengshan	49.5	126.8	528	Early	883 ± 85	13.8 ± 0.6	18.4 ± 1.3	0.7 ± 0.5
				Middle	1367 ± 170	12.1 ± 0.6	18.2 ± 1.0	1.0 ± 0.2
				Mid-late	1387 ± 206	13.7 ± 0.9	23.0 ± 1.7	2.5 ± 0.6
				Late	1133 ± 146	17.0 ± 1.2	24.3 ± 1.0	4.5 ± 1.6

measured with a VL400 instrument that measure height with ultrasound and laser (Haglof, Sweden). A total of 4325 trees were measured in the 48 plots (Table 1).

Gap fraction was measured in each plot after the plot was established. At the center of each of the five 10 × 20 m subplots, hemispherical photos were taken using a WinScanopy instrument (Regent Instruments Inc., Canadian) at 1.3 m above the ground. The photographs were taken in the morning, at dusk or when skies were cloudy to minimize the influence of direct sunshine (Ouyang et al., 2016). The digital images were processed using the WinScanopy canopy analysis software to obtain canopy structure parameters, e.g. gap fraction and canopy openness, etc. Here we used gap fraction in data analyses, but using canopy openness would get a similar result. The gap fraction of each plot was calculated as the mean value of the five measuring points.

For each plot, the maximum height and stock volume for individual trees were calculated. The timber volume (v, m^3) for each tree was calculated as: $v = a\ D^b\ H^c$, where D is diameter (cm) and H is height (m). For the coefficients (a, b and c), we used the species-specific equations provided by the national technology standard of China, "Tree volume tables (LY208-77)".

The climate data of the plots were estimated with using the models of Wang et al. (2008), which have been shown to be accurate enough through validations using independent climate data. Monthly temperature and precipitation for each plot were calculated with linear models using latitude, longitude and altitude as predictors. Then several climate indices were calculated, including potential evapotranspiration (PET) which is a widely used index for energy availability, mean annual precipitation (MAP) as indicator for water availability, and mean temperature for the coldest month (MTCM) which is a good surrogate for winter coldness. These key climate factors have been shown to be important for large-scale patterns of *D-H* and *D-N* scaling (e.g. Wang et al., 2006; Fang et al., 2012b; Lines et al., 2012). Other climate indices were closely related to these variables in our study, and thus were not included in statistic analyses to avoid collinearity.

2.2. Fitting of scaling relationships

To test MST's prediction on *D-H* and *D-N* scaling exponents (2/3 and −2, respectively) (West et al., 1999), we fitted the two scaling relationships for data from all 48 plots pooled together, and for each plot separately. Previous studies generally used data from different successional stages and climate conditions together to test MST, we examined whether this is an appropriate method. We also used the plot-level scaling exponents to test whether they showed more deviation from MST' predictions at an earlier successional stage (Prediction 1), and whether they increase or decrease during forest succession (Prediction 2.1 vs. 2.2).

For *D-H* relationship we fitted the scaling exponent as the slope of a log–log linear relationship using standard major axis (SMA) regression (Fig. 1). For *D-N* scaling, we used the maximum likelihood method to fit power law exponent with an assigned minimum D value (White et al., 2008; Clauset et al., 2009). To estimate the minimum D value (x_{min}) of each plot, we used the method of Duncanson et al. (2015). We iteratively calculated the Kolmogorov–Smirnov (KS) statistic that compared the plot's tree size distribution with a power law distribution, for increasing x_{min} starting at 5 cm (we measured trees with $D > 5$ cm). The smallest x_{min} that yielded a KS statistic with a 90th percentile probability that the data fit a power law was selected as the final x_{min}, to fit

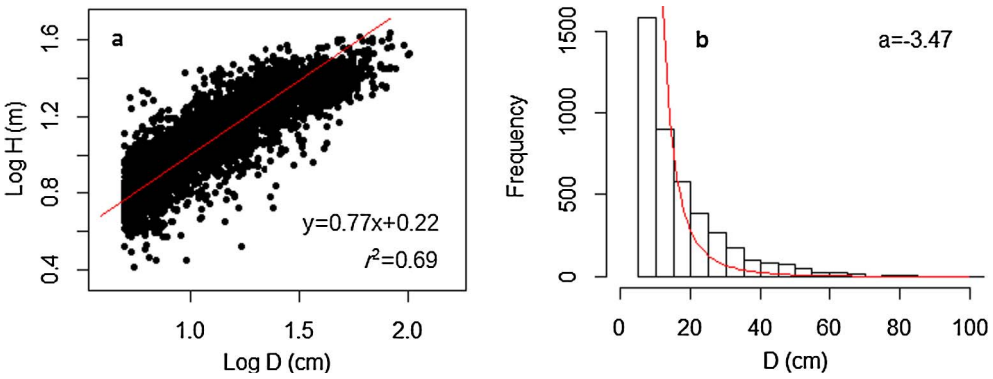

Fig. 1. Scaling relationships for data from 48 plots pooled together. (a) Relationship between height (H) and diameter at breast height (D), fitted with a log–log linear relationship using SMA regression. (b) Tree size distribution, fitted with a maximum likelihood power law.

the *D-N* scaling exponent of the plot. Meanwhile, x_{min} was also used as a proxy of recruitment limitation (see below).

2.3. Statistical analyses

To examine the potential factors affecting *D-H* and *D-N* scaling, we related the two exponents of the 48 plots to various abiotic and biotic factors. (1) Climate indices of each plot, including PET, AP and MTCM. (2) Local topography, including slope, aspect and altitude. (3) MST stress that plant size is central for a number of biological activities, including allometries (Brown et al., 2004; Niklas and Spatz, 2004). Here we used canopy height (maximum tree height) and maximum tree volume in each plot to test MST's prediction that scaling exponents should change regularly towards stands with larger trees (Niklas and Spatz, 2004). (4) We used stem density and gap fraction to indicate two different aspects of light competition. Stem density has been widely found to be a good surrogate for the intensity of competition (Kenkel, 1988, Getzin et al., 2006, Wang et al., 2016). In forest ecology it is also well known that trees are more slender in stands with higher stem density, suggesting the importance of competition on allometries (e.g. Lines et al., 2012, Wang et al., 2006). We also used gap fraction to reflect the light availability in each plot, an important aspect of light competition but has seldom been measured in large-scale studies. (5) Recruitment limitation. Skewness has long been used to quantify the asymmetry of tree size distribution and can reflect the demography difference between late successional forests and secondary forests, and along environmental gradients (Hutchings, 1997; Aiba and Kitayama, 1999; Fang et al., 2012b). Duncanson et al. (2015) also suggest that x_{min} can reflect the relative absence of small stems in a plot, and thus can be used as a proxy of recruitment limitation. However, whether these variables can well quantify the change of recruitment limitation during forest succession has seldom been tested. Here we made such a test, before using them to explain scaling relationships. (6) Successional stage, i.e. the early, middle, mid-late, and late successional stages.

We explained *D-H* and *D-N* scaling exponents with these variables, using both bivariate and multivariate analyses. Note that since the deviations from MST predictions were simply the fitted plot-level exponents minus 2/3 (*D-H* scaling) or −2 (*D-N* scaling), respectively, we were also examining whether the deviations were related to above-mentioned abiotic and biotic factors. SEM is an advanced and robust multivariate statistical method that allows for hypotheses testing of complex path-relation networks (Malaeb et al., 2000; Grace et al., 2007). Here we conducted SEM analyses based on mixed effects models, with study site as the random effect, using the "piecewiseSEM" R package (Lefcheck, 2016). We started from a full SEM (Table B.1) to test whether climate and successional stage affect scaling exponents directly, or alternatively, only affect scaling relationships indirectly via their effects on tree size (Prediction 3), or through competition and recruitment limitation (Question 3). To simplify the structure of SEM and to avoid collinearity among predictors, we dropped variables based on bivariate analyses results and Bayesian information criterion (BIC), but retained one variable for each mechanism tested in the SEM. (1) Environmental factors. Local topographic factors were excluded from SEM because bivariate analyses showed that they were weak predictors (see Section 3). The climate variables (PET, AP and MTCM) were also weak predictors in bivariate analyses. To test the indirect effect of climate on scaling exponents through biotic factors, we built a mixed effects model (with site as random effect) that explain scaling exponent with PET, AP and MTCM, and then selected variables based on BIC. The model including only MTCM had the lowest BIC than all other variable combinations, for both *D-H* or *D-N* scaling, thus MTCM was selected for the final SEMs. (2) Using a same procedure based on BIC selection, maximum stock volume instead of canopy height was selected as surrogate of tree size, and stem density instead of gap fraction was selected as indicator for light competition, for both *D-H* and *D-N* scaling. (3) Our tests showed that both skewness and x_{min} can reflect the change of recruitment limitation during forest succession (see Section 3). For *D-H* scaling, x_{min} was selected as proxy for recruitment limitation by BIC selection. For *D-N* scaling, however, we directly used skewness as the recruitment limitation proxy. This is because x_{min} was involved in the estimation of *D-N* scaling exponent and thus may not be independent (though the basic results were similar if using x_{min} to replace skewness in SEM). (4) Successional stage was converted into dummy variables to be used in SEM (Grace, 2006). The Fisher's C statistic was used to assess the SEM fits, and a P value > 0.05 suggests that the model has adequately reproduce the hypothesized causal network (Duffy et al., 2016; Lefcheck, 2016).

All statistical analyses were performed with R 3.3.1 (RDevelopment Core Team, 2007).

3. Results

3.1. Variations of scaling relationships with successional stage

When data from the 48 plots were pooled together (Fig. 1), the fitted exponent was 0.77 [95% confidence interval (CI): 0.76–0.79] for *D-H* relationship and −3.47 for *D-N* scaling, both deviated markedly from the MST prediction of 2/3 and −2.0 (West et al., 1999), respectively. We also fitted the scaling exponents for each plot separately (Fig. 2). The mean exponent was 0.75 (95% CI: 0.72–0.78) for *D-H* relationship, while −2.63 (95% CI: −2.94 to −2.32) for *D-N* scaling, again deviated significantly from the MST predictions.

However, when the plots were grouped into different successional stages (Fig. 3a and b), both the *D-H* and *D-N* scaling exponents were consistent with MST predictions in late-successional forests. Interestingly, both exponents showed greater deviation from theory predictions at earlier successional stages. Thus, our Prediction 1 was supported. The exponents decreased from early- to late-successional stages for *D-H* scaling, while increased for the *D-N* relationship.

Forest structure also changes during forest succession (Fig. 3c–h). Maximum stock volume increased markedly towards late successional forests, but the median value of canopy height did not increase much.

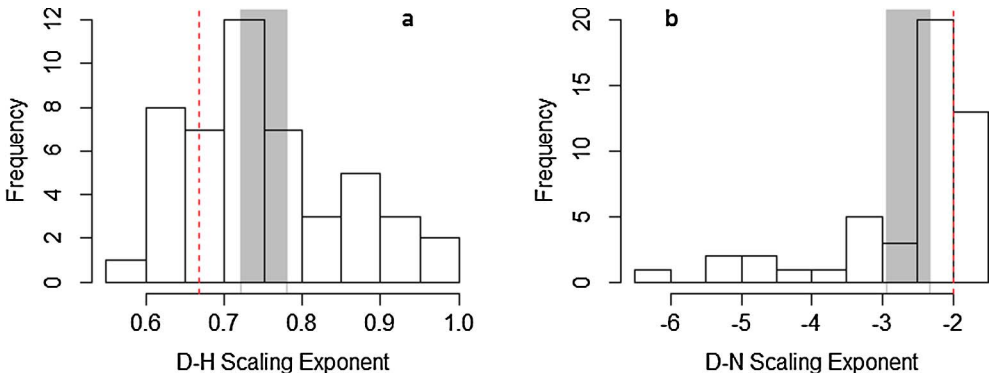

Fig. 2. Distribution of plot-level scaling exponents for (a) diameter–height (*D-H*) relationship, and (b) tree size distribution (*D-N* scaling). Red dashed lines indicate the predictions of metabolic scaling theory, and gray bars represent the 95% confidence intervals of mean scaling exponents. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

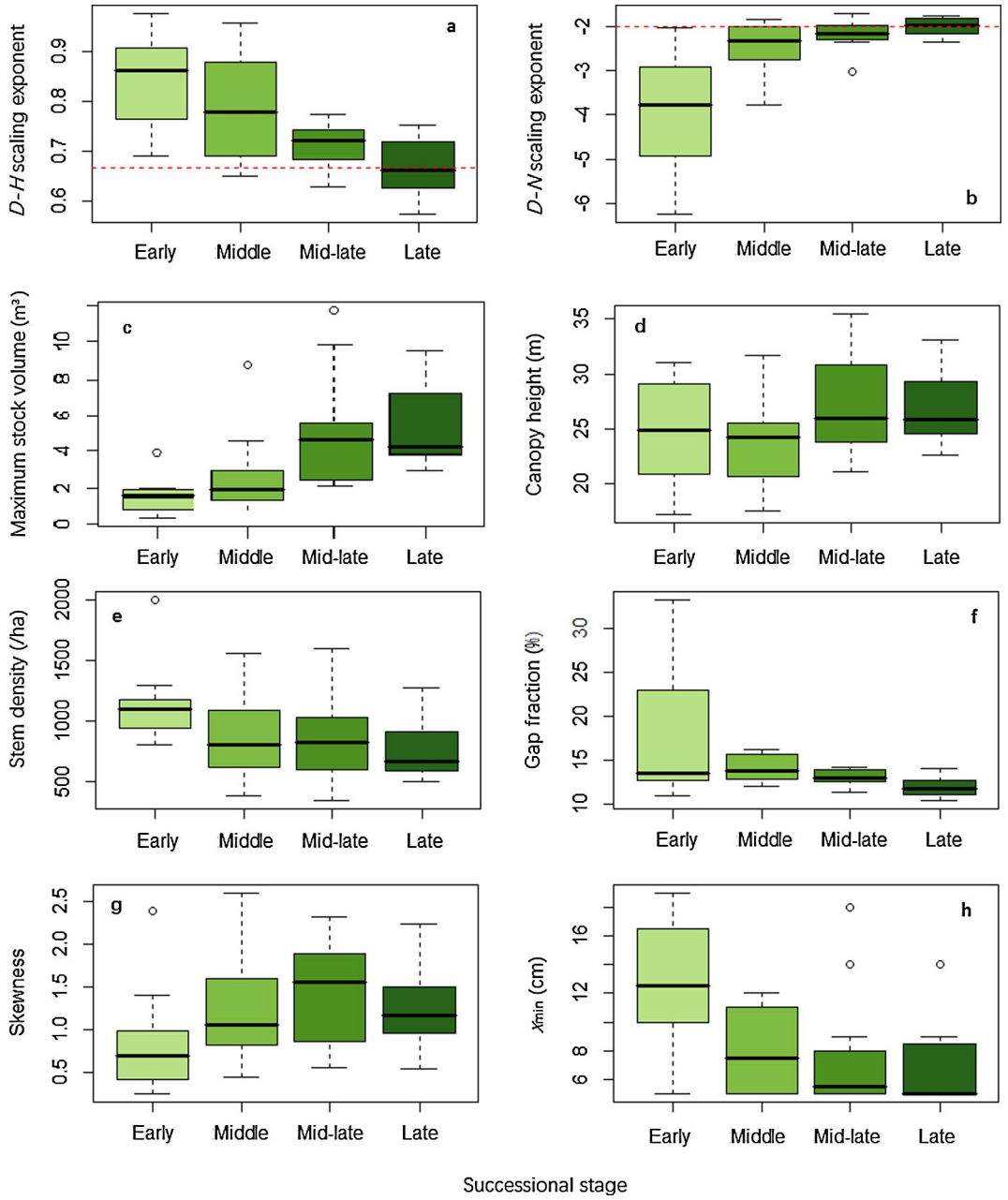

Fig. 3. Variations of plot-level scaling exponents and stand structure variables with successional stages. (a) *D-H* scaling exponent, (b) *D-N* scaling exponent, (c) maximum stock volume, (d) canopy height, (e) stem density, (f) gap fraction, (g) skewness of tree size distribution, and (h) x_{min} (see Section 2). In (a) and (b), red dashed lines indicate the predictions of metabolic scaling theory. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Stem density deceased clearly during forest succession, but the median value of gap fraction (light availability) was similar among successional stages. Skewness of *D-N* relationship increased towards late successional forests while x_{min} showed a decrease, both suggesting stronger recruitment limitation in earlier successional stages.

3.2. The effects of abiotic and biotic factors on scaling exponents

The plot-level scaling exponents did not changed significantly with latitude, for both the *D-H* and *D-N* relationships (Fig. 4). In bivariate analyses with abiotic and biotic factors (Table 2), the two exponents were also not correlated with the climate gradients of winter coldness (MTCM), energy (PET) and water availability (AP). None of the local topographic factors (altitude, slope and aspect) showed a significant relation with *D-N* exponent. In contrast, biotic factors were generally stronger correlates of the two exponents. Successional stages alone explained 45% and 52% of variations in *D-H* and *D-N* scaling exponents, respectively. In the two surrogates for tree size (Table 2, Fig. 4), maximum stock volume was negatively correlated with *D-H* exponent while positively related to *D-N* exponent, but canopy height was only positively correlated with *D-N* exponent. As for the two variables related to light competition, stem density was positively related to *D-H* exponent but negatively related to *D-N* exponent, and gap fraction also revealed a negative correlation with *D-N* exponent. For the two proxies of recruitment limitation, skewness was positively related with *D-N* exponent; x_{min} was positively correlated with *D-H* scaling exponent but negatively related to *D-H* exponent.

The SEMs after BIC selection of variables were shown in Fig. 5. A test with Fisher's *C* showed that the *P* value was 0.61 and 0.12 for the *D-H* and *D-N* scaling SEM, respectively, suggesting very good model fits. SEMs revealed that *D-H* scaling was significantly affected by stem density and successional stage, while *D-N* scaling was directly affected

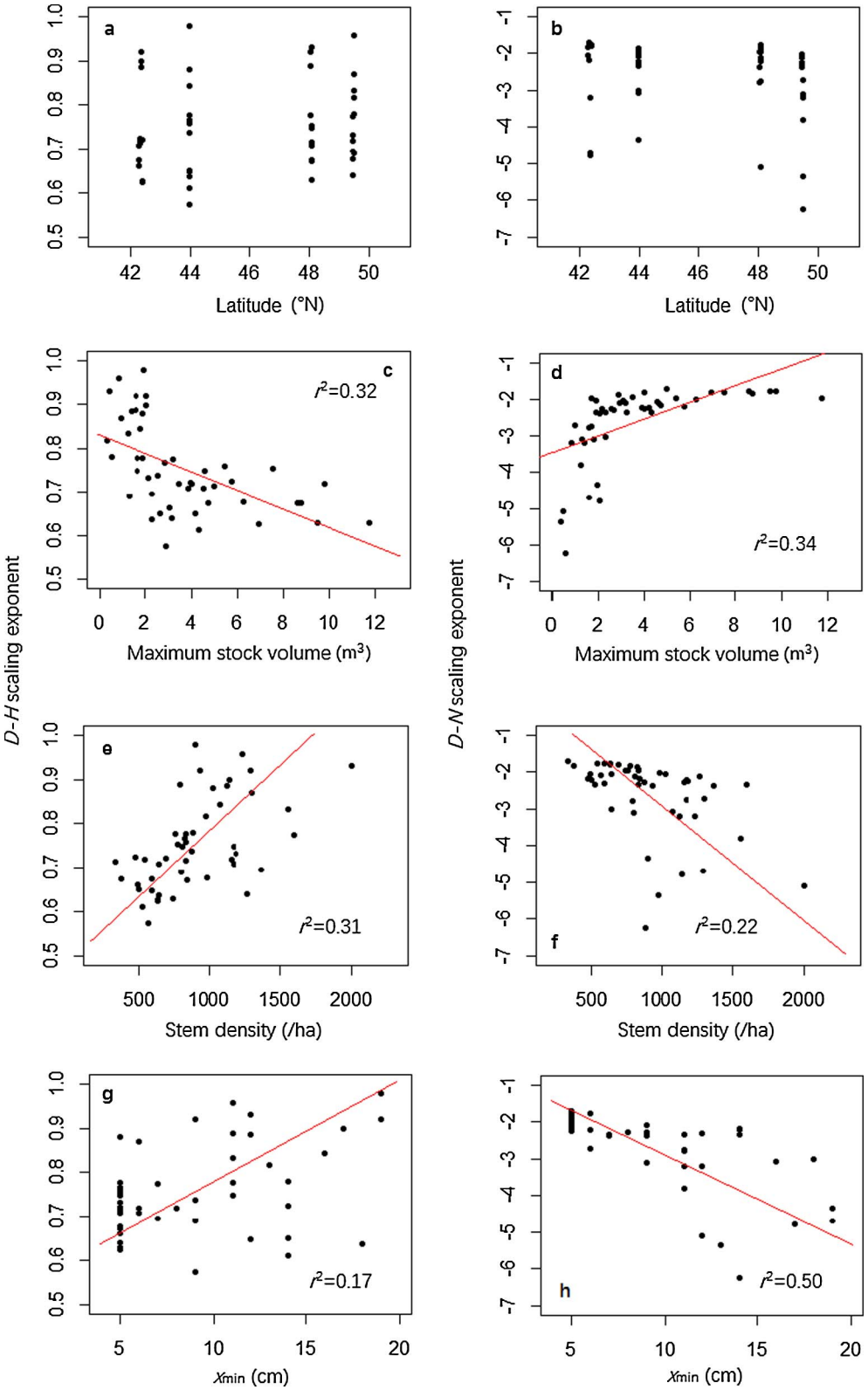

Fig. 4. Relationship of *D-H* and *D-N* scaling exponents with latitude (a and b), maximum stock volume (c and d), stem density (e and f), and x_{min} (g and h). Regression lines were given for relationships significant at $P < 0.05$.

by skewness and successional stage. Maximum stock volume did not have direct effect on both scaling exponents. Thus, the Prediction 3 that climate and successional stage affects scaling exponents via tree size was not supported. Climate (MTCM) also had no direct influence on scaling exponents, but MTCM and successional stage showed indirect effects through stem density (*D-H* scaling) or skewness (*D-N* scaling).

4. Discussions

In this analysis, we aimed to examine how scaling relationships deviate from MST predictions across latitudinal gradient and successional stages, and to examine the potential factors leading to these deviations. These questions are important for testing MST in a correct way, and for improving MST to better model the widely observed

Table 2
The r^2 of each of the abiotic and biotic factors in explaining the *D-H* and *D-N* scaling exponents of the 48 plots. MTCM, mean temperature for the coldest month; MAP, mean annual precipitation; PET, potential evaporation.

	D-H scaling exponent	*D-N* scaling exponent
Latitude	0.01	−0.03
Abiotic factors:		
Climate		
MTCM	−0.01	0.03
MAP	−0.02	0.02
PET	0.00	0.00
Local topography		
Altitude	−0.02	0.02
Slope	0.02	0.04
Slope aspect	0.17	0.16
Biotic factors:		
Successional stage	0.45 ***	0.52 ***
Size		
Maximum stock volume	−0.32 ***	0.34 ***
Canopy height	−0.02	0.14 **
Light competition		
Stem density	0.31 ***	−0.22 ***
Gap fraction	0.02	−0.34 ***
Recruitment limitation		
Skewness	−0.07	0.16 **
x_{min}	0.17 **	−0.50 ***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

change of scaling relationships across forest types and environmental gradients.

4.1. Changes of allometric relationships with successional stages

At a first glance, our results seem to support the criticisms of MST: Figs. 1 and 2 show that both scaling exponents deviate clearly from MST predictions. However, when examined for each successional stage separately, a different pattern emerged (Fig. 3). Scaling exponents in the late successional forests were consistent with MST predictions, for both *D-H* and *D-N* relationships. On the other hand, in disturbed forests the two exponents showed greater deviation from MST predictions at an earlier successional stage, exactly as expected by Prediction 1. This confirms the idea that MST only predicts scaling exponents for steady-state forests, and that deviations from MST predictions can be explained by violations of assumptions (Cassemiro and Diniz-Filho, 2010; Duncanson et al., 2015; Farrior et al., 2016). Many studies tested MST with plots from various successional stages pooled together (as in Figs. 1 and 2). We showed that, using this method it is very likely to found that MST was not supported. Thus, datasets including secondary forests cannot be used to falsify MST, because MST's assumptions (steady state forests without external disturbance and recruitment limitations) were not met.

As for whether the two exponents increase towards late successional forests (Prediction 2.1), our results showed that the *D-N* scaling exponent did showed an increase, but the *D-H* exponent decreased towards late successional forests (Fig. 3) and was not related to forest height (Table 2). Prediction 2.1 is based on the assumption that shorter forests are generally younger, but we found that canopy height does not necessary increase much during forest succession (Fig. 3d, see also Table 1), and thus Prediction 2.1 was not supported. This also suggests that forest height may not be a good indicator to discriminate successional status at a large scale. Note that, forest height is well known to change significantly with climate and site quality even for a same forest type (e.g. López-Serrano et al., 2005). On the other hand, we showed that maximum tree volume increased markedly across successional stages (Fig. 3c). This suggest that the change in tree size during forest succession is also strongly affected by tree diameter, instead of by height alone. Thus stock volume (or biomass) may be better indicator of tree size compared with height.

In our results, *D-H* exponent is negatively related to maximum stock volume (Fig. 4c). This is consistent with the MST prediction that *D-H* exponent should decrease with plant size (Niklas and Spatz, 2004; Enquist et al., 2007a), and thus Fig. 3a seem to support Prediction 2.2. However, our SEMs showed that the effect of maximum stock volume on both exponents was not significant (Fig. 5). Thus the decrease of *D-H* scaling exponent towards late successional forests is not mainly caused by changes in tree size, and we conclude that Prediction 2.2 was also not well supported.

4.2. The effects of climate and size on scaling relationships

Previous studies have found that scaling exponents were significantly correlated with climate factors, for both *D-H* and *D-N* relationships (Wang et al., 2006; Fang et al., 2012b; Lines et al., 2012; Duncanson et al., 2015; Hulshof et al., 2015). These findings were generally viewed as unfavorable evidence for MST. However, if a significant correlation between climate and scaling exponent was cause by the change of tree size with climate, instead of by climate directly, then MST cannot be falsified (see Section 1). In our study, none of the climatic and local environmental factors was good correlate of *D-H* and *D-N* scaling (Table 2). The SEMs also showed that the direct effect of climate was not significant for both exponents (Fig. 5). These results support a key idea of MST that allometric exponents are not very sensitive to environmental gradients (Enquist and Niklas, 2001; Niklas and Enquist, 2001). Our results are different from above-mentioned studies that found significant correlations between climate and allometries, probably because the climate gradient here is not large enough compared with theirs. Thus whether climate affect scaling exponents directly still need further tests at a broad scale. However, our plots covered a latitudinal range of ca. 7° (42.4–49.5°N), which is clearly not a short climate gradient. Consequently, our results at least suggest that the direct influence of climate on scaling relationships are rather weak.

Our results also suggest the necessity to test MST with a hypothesis-testing statistic approach, with different potential mechanisms included simultaneously. Correlative analyses are not reliable methods to test hypotheses, which is evident in this study. For instance, climate was not correlated with both scaling exponents (Table 2), but the SEMs revealed that it affects scaling relationships indirectly through stem density or skewness (Fig. 5). On the other hand, maximum stock volume was significantly correlated with both scaling exponents (Fig. 4). However, the SEMs showed that it did not have significant effect when other mechanisms were included in the model simultaneously. Thus, the Prediction 3 derived from MST studies (Niklas and Spatz, 2004) was not supported, because the variations of scaling relationships across latitudinal gradient and successional stages were not mainly explained by changing exponents with tree size. This suggests that other ecological processes not included in present MST are needed to explain the deviations from MST.

4.3. The role of successional stage, stem density and community demography

An interesting finding of this study is that the deviations from MST predictions were closely related with stem density and skewness of tree size distribution (Fig. 4e–h). The SEMs further revealed that the major

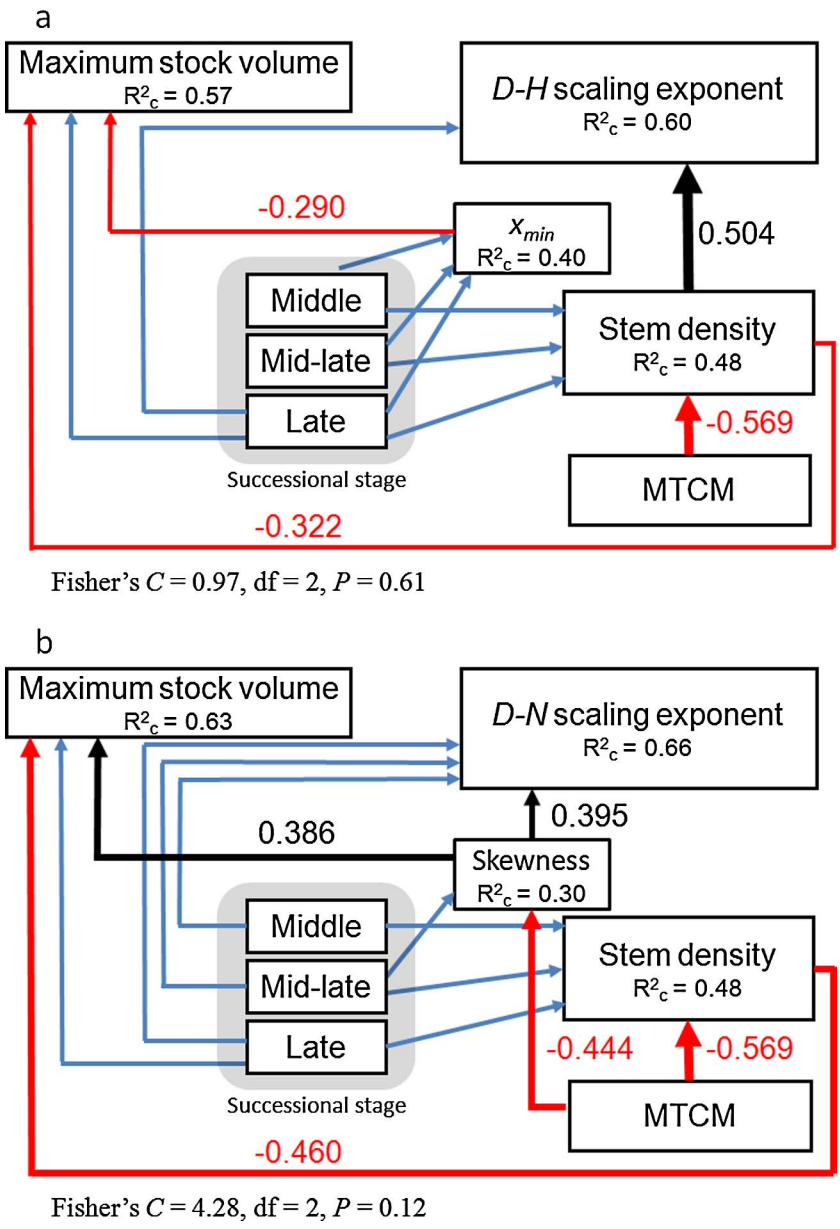

Fig. 5. Structure equation models for the effects of climate (MTCM), successional stage, size (maximum stock volume), competition (stem density) and recruitment limitation (x_{min} or skewness) on two allometric exponents: (a) *D-H* scaling, and (b) *D-N* scaling. Non-significant pathways were not shown ($P \geq 0.05$). Black arrows denote positive relationships while red arrows for negative ones, with standardized path coefficients reported. Blue arrows denote the paths of dummy variables for successional stages, and their standardized coefficients were not shown for clarity (see Appendix B for details). The R_c^2 for each component model is given in the box of response variable. R_c^2 is based on the variance of both the fixed and random effects (Lefcheck, 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

factors leading to these deviations differed between scaling relationships, with stem density critical for *D-H* allometry while skewness crucial for *D-N* scaling (Fig. 5).

Asymmetric competition for light has long been known to be important for *D-H* allometry in local scale studies (e.g.Ogawa, 1969; Thomas, 1996). Our finding that *D-H* exponent decrease towards late successional forests is consistent with the fact that: light availability did not differed much among successional stages (Fig. 3f), but stem density is much higher in earlier successional forests (Fig. 3e). That is, competition for light is more intensive in earlier successional stages. Consequently, trees there need to invest more on height growth relative to diameter growth, and thus are more slender. Our results are in line with many previous studies that higher stem density intensify light competition between trees (e.g. Getzin et al. 2006, Wang et al., 2016), and that trees are more slender in stands with higher stem density due to the effects of competition on *D-H* allometries (e.g. Lines et al., 2012; Wang et al., 2006). Some studies have pointed out that MST ignored the importance of competition for resources such as light and nutrient. They demonstrated that another prediction of MST (the scaling of tree growth with size) is only valid when competition for light is not important (Muller-Landau et al., 2006; Coomes and Allen, 2009; Rüger and Condit, 2012). Our results add evidence to this idea, showing that MST was not supported when light competition is intensive (in earlier successional forests). Meanwhile, previous studies generally found that conifers had a higher *D-H* scaling exponent than broadleaf trees because of differences in wood density or branching architecture (Lines et al., 2012; Duncanson et al., 2015; Hulshof et al., 2015). In our study, late successional forests were dominated by Korean pine while secondary forests dominated by broadleaf trees, thus from their results it seems that late successional forests should have higher *D-H* exponent. However, we observed a converse pattern (Fig. 3a). This suggests that the influence of light competition on *D-H* scaling is much stronger than the

structural differences between conifers and broadleaf trees in our study, again confirms that competition is a critical mechanism affecting allometric relationships.

Previous studies have suggested that recruitment limitation may affect scaling relationships (Allen et al., 2008; Duncanson et al., 2015). However, its influence has seldom been quantified and used to explain scaling exponents. Consequently, the relative effects of recruitment limitation vs. other factors (e.g. competition and tree size) is still unclear. Here we made an attempt to quantify recruitment limitation using two proxies: skewness and x_{min}. It is well known that late successional forests have little recruitment limitation, as indicated by a "reverse J-shaped" size distribution with far more small trees than large ones (which means high skewness and low x_{min}). In contrast, early-successional forests typically have a hump-shaped size distribution that lack small trees, which indicates clear recruitment limitations (i.e. low skewness but high x_{min}). Our results showed that these differences in recruitment limitation among successional stages were well reflected by the two proxies: skewness increased regularly towards late successional forests while x_{min} showed a decrease (Fig. 3g and h). This suggests that the two variables can be well used as proxies of recruitment limitation in future works. Our SEM results show that recruitment limitation is key for the deviation of *D-N* scaling from MST (Fig. 5). Similarly, Allen et al. (2008) also found that the size-frequency distribution in desert shrub stands deviate strongly from MST predictions due to recruitment limitation. They further showed that the deviation was related to precipitation, consistent with our results that climate lead to *D-N* scaling change through skewness (Fig. 5b), and supporting the idea that deviations from MST can be partly explained by environmentally driven recruitment limitations (Duncanson et al., 2015). In another study, Issoufou et al. (2015) also found that MST can describe several other allometric relationships in mature shrub stands without disturbance, but annual clear cutting drives scaling relationships to deviate from MST predictions because of intensive regeneration processes.

In the SEMs, successional stage also showed direct effect on scaling exponents (Fig. 5), suggesting that the change of allometry with successional stages is not only caused by stem density or skewness, and are related to other factors. For instance, early-successional forests are dominated by light-demanding pioneer species while late-successional forests are dominated by shade-tolerant trees. Such differences may affect both competition intensity (e.g. Coomes and Allen, 2007) and regeneration dynamics, but cannot be reflected by stem density and skewness. Further studies are still needed to better quantify these influences of successional stage on scaling relationships.

5. Conclusions and implications

In this analysis, we tested several hypothesis related to MST, using forest plots across latitudinal gradient and successional stages in northeast China. On one hand, we found that MST did gain supports in late successional forests where the model assumptions were not violated. This suggests MST as a good baseline to develop future general allometry models including both disturbed and undisturbed forests. On the other hand, our results do not support a hypothesis of MST, which suggests that geographic variations of allometries can be explained by changes in tree size with climate and successional status. We find it interesting that scaling exponents deviate from MST predictions in a fairly predictable way: the deviations increase regularly as model assumptions are more severely violated in earlier successional forests (Fig. 3a and b). Further, our results suggest that these deviations may be caused by ecological processes not yet considered in MST: competition, recruitment limitation, and other differences among successional stages (Figs. 4 and 5). We suggest future researches to further examine the influence of these processes on scaling relationships, which is critical for improving the ability of MST to model scaling relationships in disturbed forests. Secondary forests account for most of the forest area in China and many other regions of the world, and they have great potential in carbon sequestration because of higher growth rate compared with late successional forests. Thus, improving the ability of MST to model allometries in secondary forests should provide very useful tools for forest carbon estimation and management.

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Appendix A

See Fig. A.1

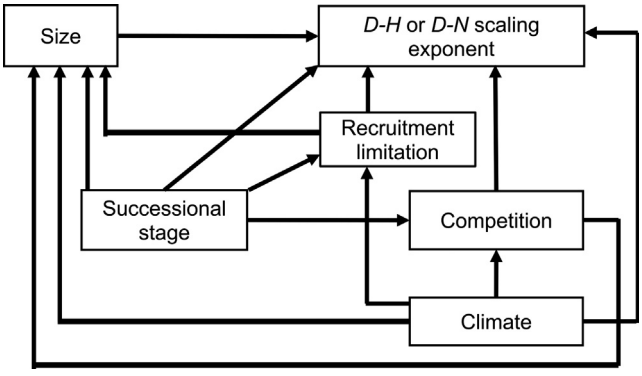

Fig. A.1. Full structure equation models for the potential pathway of climate, successional stage, tree size, competition and recruitment limitation in affecting *D-H* or *D-N* scaling exponents. This full model is designed to test the direct effects of above-mentioned factors on scaling exponent, and the indirect effects of climate and successional stage through tree size, competition and recruitment limitation (see Section 1).

Appendix B

See Table B.1

Table B.1
Standardized coefficients (scaled by mean and variance), standard errors, and *P*-values for the structure equation models (SEM), which test the effects of MTCM (mean temperature for the coldest month), successional stage, size (maximum stock volume), competition (stem density) and recruitment limitation (x_{min} or skewness) on *D-H* or *D-N* exponent. Variables significant at $P < 0.05$ are boldfaced.

Response	Predictor	Estimate	Standard error	*P*-value
***SEM for D-H* scaling**				
D-H scaling exponent	log (Stem density)	0.504	0.147	**0.002**
	Successional stage			
	Middle	0.149	0.320	0.644
	Mid-late	−0.562	0.337	0.104
	Late	−0.907	0.353	**0.014**
	x_{min}	0.183	0.130	0.169
	Maximum stock volume	−0.017	0.151	0.909
	MTCM	0.139	0.147	0.349
log (Stem density)	MTCM	−0.569	0.108	**0.000**
	Successional stage			
	Middle	−0.868	0.303	**0.007**
	Mid-late	−0.942	0.303	**0.003**
	Late	−1.088	0.303	**0.001**
Maximum stock volume	log (Stem density)	−0.322	0.140	**0.027**
	x_{min}	−0.290	0.124	**0.025**
	Successional stage			
	Middle	−0.168	0.323	0.606
	Mid-late	0.640	0.331	0.061
	Late	0.709	0.345	**0.047**
	MTCM	0.088	0.192	0.648
x_{min}	Successional stage			
	Middle	−1.065	0.336	**0.003**
	Mid-late	−1.150	0.336	**0.002**
	Late	−1.282	0.336	**0.001**
	MTCM	0.235	0.211	0.272
***SEM for D-N* scaling**				
D-N scaling exponent	Skewness	0.395	0.127	**0.004**
	Successional stage			
	Middle	0.942	0.292	**0.003**
	Mid-late	1.040	0.312	**0.002**
	Late	1.267	0.317	**0.000**
	Maximum stock volume	0.055	0.148	0.710
	log (Stem density)	−0.192	0.149	0.205
	MTCM	0.246	0.148	0.104
log (Stem density)	MTCM	−0.569	0.108	**0.000**
	Successional stage			
	Middle	−0.868	0.303	**0.007**
	Mid-late	−0.942	0.303	**0.003**
	Late	−1.088	0.303	**0.001**
Maximum stock volume	log (Stem density)	−0.460	0.136	**0.002**
	Skewness	0.386	0.116	**0.002**
	Successional stage			
	Middle	−0.231	0.299	0.444
	Mid-late	0.495	0.315	0.125
	Late	0.686	0.313	**0.035**
	MTCM	0.125	0.203	0.539
Skewness	MTCM	−0.444	0.126	**0.001**
	Successional stage			
	Middle	0.657	0.352	0.069
	Mid-late	0.907	0.352	**0.014**
	Late	0.635	0.352	0.078

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