Effects of inter-specific variability on biomass allocation: A hierarchical Bayesian approach

You-Shi Wang a, Cheng-Jin Chu b,⁎, Kai Zhu c, Ze-Hao Shen d

Abstract

The partitioning of total biomass among plant organs (stem, leaf, root, and shoot, respectively) has been a central topic in functional ecology. Many studies referring to inter-specific biomass allocation mainly concentrate on the completely pooled data treating all species involved equivalently. Less work has incorporated species differences into such allocation patterns. In the present paper, we explored the potential effects of species variability on biomass allocation patterns in a hierarchical Bayesian framework, which assigned individual species separate allometric values, drawn from ‘global’ parameters on the community level. Results demonstrated that the inclusion of species identity could significantly decrease the allocation slopes compared to those from the corresponding non-hierarchical models on pooled data, and much less residual variation was left for hierarchical models. Our work exhibits the importance of species variability on biomass partition and the potential impact of sample size on allometric estimates, and indicates that the inclusion of certain complexity such as species difference is a necessary step to better understand the scaling theories in ecology.

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1. Introduction

Biomass allocation among different vegetative organs, such as leaves (M L ), stems (M s ), roots (M r ) and shoots (M sh ), has been a central question in plant ecology, due to its importance to life-history theory and community dynamics (Tilman, 1988; McConnaughay and Coleman, 1999). Based on the flow of resources through networks, Niklas and Enquist (2002a, b) reported that $M_r \propto M_s^{3/4} \propto M_{sh}^{3/4}$. Usually, the pooled data from different species are used in studies of biomass allocation, the implicitly underlying assumption of which is that there are no differences among species (Niklas and Enquist, 2002a, b; Niklas, 2004). If this is not true, we could mis-categorize such differences into random variability, which could result in biased inference and further biased prediction (Clark, 2007; Dietze et al., 2008). Actually, substantial differences among species are commonplace in nature, and consequently exert pronounced impact on populations and communities (Tilman, 1988; Clark, 2007; Melbourne and Hastings, 2008). Additionally, some studies have also argued that such species heterogeneity could significantly influence the allometric parameters of scaling laws (such as Lovegrove, 2003). Thus the inclusion of species variation into allometric scaling research is necessary (White et al., 2007).

There are different methods to incorporate such inter-specific variability into data analysis, both in frequentist (e.g. lm4 package in R software; Qian, 2009) and Bayesian statistics (Clark, 2007; Gelman and Hill, 2007). Due to the recently emerging application of Bayesian approaches in ecological research (Clark, 2007; Dietze et al., 2008; Price et al., 2009), in the present paper we chose the hierarchical Bayesian models (HB), which can readily accommodate multiple sources of uncertainty (Congdon, 2007). Hierarchical models present a way to estimate separate parameters for individual species, while simultaneously fitting ‘global’ parameters across species that constrain the species-specific relationships (Dietze et al., 2008; Price et al., 2009).

Dietze et al. (2008) has constructed a HB framework to exploit the allometric relationships between tree diameter at the breast height and other related properties (such as tree height, canopy depth and radius), which has been expanded by Price et al. (2009). As far as we are aware, however, there have been few studies to test biomass allocation in a HB framework to account for the species identity. In the present work, we developed such HB models to test the potential importance of species differences on allocation patterns, compared to the corresponding simple models on pooled data. In the Discussion, we further explored the potential effect of sample size on the allometric exponents.
2. Materials and methods

2.1. Data description

Our biomass data were freely downloaded from ORNL DAAC (http://daac.ornl.gov/), previously compiled by Karl J. Niklas, which consist of two parts: Cannell (1982) and Niklas data (Niklas and Enquist, 2002a, b; Niklas, 2004). A detailed description of the combined dataset was presented in both Niklas and Enquist (2002a, b) and Niklas (2004). Briefly, these datasets report stand-level mean biomass of species for stems, leaves, roots and shoots, respectively, from direct measurements of fully dissected representative plants. Not all species have complete records for four organs mentioned above, as a result, we have 175 species and 1124 observations for leaf vs stem analyses, 121 species and 684 observations for leaf vs root analyses, 117 species and 717 observations for stem vs root analyses, and 176 species and 1244 observations for shoot vs root analyses, respectively.

2.2. HB model

The power-law relationship for biomass allocation is as follows:

\[ y = b_0 x^b \]

\[ \log y = \log b_0 + b_1 \log x \]

where \( y \) and \( x \) are variables for organs, \( b_0 \) is the allometric constant, \( b_1 \) is the scaling exponent (e.g. Huxley, 1932; Niklas and Enquist, 2002a, b).

Based on Eq. (1), for simple Bayesian models (SB) with pooled data we have the following allometric formula:

\[ Y_i \sim N(X_i \beta, \sigma^2) \]

where \( Y_i = \log(y_i) \), \( X_i = [1 \ \log(x_i)] \), \( \beta = [\log(b_0), b_1]^T \), and \( \sigma^2 \) are normally distributed residual variability of allometric models. Subscript \( i \) denotes fitting for each individual.

In order to allow the species differences, we should estimate separate allometric parameters for individual species, which are constrained by the ‘global’ parameters (\( \beta^{(g)} \) below with the dimension of \( 2 \times 1 \)). Then we have the following individual equation of \( \beta \) for different species:

\[ \beta_j \sim N_2(\beta^{(g)}, \sum) \]

where subscript \( j \) denotes fitting for each species, \( \sum \) is a \( 2 \times 2 \) covariance matrix, and \( N_2 \) represents the bivariate normal distribution.

The allometric equation for each species incorporating the species identity is

\[ Y_{ij} \sim N(X_{ij} \beta_{ij}, \sigma^2) \]

where \( \sigma^2 \) is the normally distributed residual variance of allometric models after having accounted for species differences. Subscript \( ij \) denotes fitting for individual \( i \) of species \( j \). For all parameters involved in models, non-informative conjugate priors were used (Clark, 2007).

We carried out Markov chain Monte Carlo (MCMC) simulations to fit above pooled linear regression (SB) and random effect regression models (HB) for each of the four pairs of plant organs (leaf vs stem, leaf vs root, stem vs root, and shoot vs root, respectively), to reach the total 8 allometric models. Through R2WinBUGS package (Sturtz et al., 2005), Gibbs sampling was implemented in WinBUGS 1.4 (Lunn et al., 2000), and others were conducted in R 2.9.1 (R Development Core Team, 2009).

Each model was run for 200,000 iterations and 3 chains with different initial values for parameters. We discarded those initial 100,000 samples as the burn-in consideration. Convergence was observed graphically for all parameters and diagnosed using Brooks–Gelman statistic (Brooks and Gelman, 1998). The remaining converged MCMC samples were thinned every 100 to reduce autocorrelations. So for each model, we had a posterior sample size of 3000 (1000×3 chains). Based on these thinned samples, we calculated parameter estimates and corresponding credible intervals.

To compare the performances of HB and corresponding SB models to fit the observed data, we estimated the deviance information criterion (DIC) (Spiegelhalter et al., 2002), which was directly generated by WinBUGS software. The lower the DIC scores, the better the models.

3. Results

In our MCMC simulations, all parameters were well converged. We compared the posterior distributions for ‘global’ parameters of biomass allocation for HB models to the counterparts of corresponding SB ones. Results exhibited that the inclusion of species differences significantly decreased the slopes (the 95% BCI s of slopes from HB did not overlap with the ones from SB), except for stem vs root and leaf vs root (Fig. 1, Table 1). We further estimated the random species effects (Fig. 2), which indicated that the variability among some species was notable.

On the predicted vs observed plots, the complex models (HB) behaved better with points closely distributed along the 1 : 1 line than the simple models (SB) (the goodness-of-fit; results not shown here). However, improved complexity could sometimes ignite the over-fitting issue. The balanced statistics DIC not only captured the goodness-of-fit, but also considered model complexity with a penalty term. In our simulations, hierarchical versions of four allocation models had much lower DIC scores than those from corresponding simple Bayesian versions (Table 2).

4. Discussion

The incorporation of species differences notably decreased the ‘global’ allometric parameters of biomass allocation except for stem vs root and leaf vs root (with the decreasing trends but not significant.
which may be due to the relatively low species number and/or observations) (Fig. 1, Table 1), which indicated that the species identity could have pronounced impact on inter-specific biomass allocation patterns. As we know, with the unbalanced dataset in HB models species with small number of individuals could borrow strength from ones with large sample size (Clark, 2007). To explore the underlying mechanism for the decreasing-slope patterns observed, we attempted to figure out the relationship between predicted slope for each species inferred from HB and sample size (Fig. 3). The result demonstrated that species with large sample size usually had relatively small allometric slopes, which made the global-level slopes closer to 0 in HB than found when species were pooled in SB. Though HB models presented here were more complicated, the inclusion of species identity did result in a better explanation of observed data (the lower DIC scores), so were preferred.

In allometric scaling theories, another common phenomenon is that usually there is relatively large residual variation left unexplained (Brown et al., 2004). In our work, the unexplained residual variance for SB models was on average 0.140 ($\sigma^2$ in Eq. (2), comparing to 0.033 ($\omega^2$ in Eq. (4) in HB models (Table 2). This further demonstrated that species variability could be an important source of uncertainty for mass partition.

There have been many studies critical of the existence of universal allometric scaling exponents (Savage et al., 2004; White et al., 2007; Isaac and Carbone, 2010). It has demonstrated that many factors such as phylogeny (Sieg et al., 2009), metabolic states (e.g. rest, field, and exercise) (Glazier, 2009), growth habitats (Deng et al., 2006) and statistical methods (Sieg et al., 2009) could influence the assessments of the allometric slopes. Though in the present paper we did not find the strong support for nor against such universal-exponent argument (Table 1), we did exhibit the potential effects of species differences and sample size on the biomass allocation, which have been recently considered as potentially important aspects in scaling laws (Coomes and Allen, 2009; White et al., 2007).

It should be noted that we did not fit multiple-response variables (stem, leaf, and shoot vs root, respectively) simultaneously. As there

<table>
<thead>
<tr>
<th>Model</th>
<th>Leaf vs stem</th>
<th>Stem vs root</th>
<th>Leaf vs root</th>
<th>Shoot vs root</th>
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</thead>
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<tr>
<td>DIC</td>
<td>722.56</td>
<td>120.89</td>
<td>376.36</td>
<td>435.57</td>
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<tr>
<td>UR</td>
<td>0.026</td>
<td>0.041</td>
<td>0.028</td>
<td>0.035</td>
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</tbody>
</table>

**Table 1**
Posterior mean, standard deviation (SD) and 95% Bayesian credible intervals (BCI) of slopes for hierarchical Bayesian (HB) models and the corresponding simple Bayesian (SB) models. “Theoretical” column is from Niklas and Enquist (2002a, b), and Niklas (2004).

<table>
<thead>
<tr>
<th>Theoretical</th>
<th>Model</th>
<th>Observed</th>
<th>BCI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf vs stem</td>
<td>HB</td>
<td>0.711</td>
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<td></td>
<td>SB</td>
<td>0.750</td>
<td>0.004</td>
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<td></td>
<td>SB</td>
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<td>0.019</td>
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<td></td>
<td>SB</td>
<td>0.824</td>
<td>0.007</td>
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<tr>
<td>Shoot vs root</td>
<td>HB</td>
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<td>0.018</td>
</tr>
<tr>
<td></td>
<td>SB</td>
<td>1.049</td>
<td>0.005</td>
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</tbody>
</table>

**Table 2**
The deviance information criterion (DIC) and the posterior means for the unexplained residual (UR) variances for hierarchical Bayesian models (HB) and the corresponding simple Bayesian models (SB).
Acknowledgements

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References