



Short communication

Are allometric model parameters of aboveground biomass for trees phylogenetically constrained?

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ABSTRACT

Knowledge of which biological and functional traits have, or lack, phylogenetic signal in a particular group of organisms is important to understanding the formation and functioning of biological communities. Allometric biomass models reflecting tree growth characteristics are commonly used to predict forest biomass. However, few studies have examined whether model parameters are constrained by phylogeny. Here, we use a comprehensive database (including 276 tree species) compiled from 894 allometric biomass models published in 302 articles to examine whether parameters a and b of the model $W = aD^b$ (where W stands for aboveground biomass, D is diameter at breast height) exhibit phylogenetic signal for all tree species as a whole and for different groups of tree species. For either model parameter, we relate difference in model parameter between different tree species to phylogenetic distance and to environmental distance between pairwise sites. Our study shows that neither model parameter exhibits phylogenetic signals (Pagel's λ and Blomberg's K both approach zero). This is the case regardless of whether all tree species in our data set were analyzed as a whole or tree species in different taxonomic groups (gymnosperm and angiosperm), leaf duration groups (evergreen and deciduous), or ecological groups (tropical, temperate and boreal) were analyzed separately. Our study also shows that difference in each parameter of the allometric biomass model is not significantly related to phylogenetic and environmental distances between tree species in different sites.

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1. Introduction

Many biological and functional traits are restricted to one or a few major clades (e.g., orders and families) on the one hand and are commonly shared by member taxa within the clades on the other hand; therefore, they carry phylogenetic signal. Phylogenetic signal has been detected in a number of studies (Losos, 2008). For example, for animals, phylogenetic signal has been detected in host use in diet in non-snake squamates (Vitt and Pianka, 2005), fish parasites (Desdevises et al., 2002), herbivore identity among host plants (Weiblen et al., 2006), ecological determinants of lake occupancy in sunfish (Helmus et al., 2007) and climatic niche among neotropical hyliid frogs (Wiens et al., 2006). For plants, phylogenetic

signal has been detected in ecophysiological traits among European plants (Prinzing et al., 2001), growth form and habitat use among plant species in Costa Rican rainforests (Chazdon et al., 2003), susceptibility to fungal pathogens in Panamanian trees (Gilbert and Webb, 2007), mortality of seedlings in a Bornean rain forest (Webb et al., 2006), and growth form among seed plant families worldwide (Qian and Zhang, 2014). However, lack of phylogenetic signal in biological and functional traits has also been reported in a number of studies, including habitat use, activity time and prey size in a community of Cuban Anolis lizards (Losos, 2008), and niche overlap and habitat use in Florida oaks (Cavender-Bares et al., 2004) and English meadow plants (Silvertown et al., 2006a, 2006b). Furthermore, there are a number of studies showing mixed results. For example, Vitt et al. (1999) found that similarity in diet is related to phylogenetic similarity in Amazonian lizards, but the relationship between similarity in habitat use and phylogeny is not significant. Knowledge of which traits have, or lack, phylogenetic

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signal in a particular group of organisms is important to understanding the formation and function of biological communities.

Allometry studies the relationship of body size to, among other things, shape, anatomy, physiology, and behaviour (Damuth, 2001). Allometric scaling is one of the key study components in biology, ecology, and forestry. Pantin (1932) pointed out that most size-related variation can be described by so-called allometric equations, which are power functions of the form: $Y = Y_0 M^b$ (Brown et al., 2004). The equation relates some dependent variable, Y , such as metabolic rate, development time, population growth rate, or rate of molecular evolution, to body mass, M , through two coefficients, a normalization constant, Y_0 , and an allometric exponent, b (Brown et al., 2004). This equation has been broadly used to estimate forest aboveground biomass (W) of trees based on diameter at breast height (D): $W = aD^b$, where a and b are coefficients to be estimated. Previous studies have shown that the two coefficients (i.e., a and b) vary greatly between tree species. However, no studies have investigated whether the two coefficients have phylogenetic signal. Knowledge of the relationship between similarity of either coefficient and phylogenetic relatedness between tree species is important to accurately estimating forest biomass, on which many studies of the effect of global change on forest ecosystems depend. This is because far fewer than 10% of about 61,000 tree species worldwide (Qian et al., 2019) have had their coefficients being estimated. On the one hand, if there are strong phylogenetic signal in the two coefficients, researchers and foresters can determine how to select existing parameterized models to predict biomass for those tree species whose model coefficients are not available yet, based on phylogenetic relatedness between those species which have already had model coefficients and those which do not. Information on phylogenetic relatedness of the model parameters can be useful when applying models to predict forest carbon variation due to global warming. On the other hand, if there is no phylogenetic signal in the two model parameters, researchers and foresters may search for other models that can well predict biomass and whose parameters carry phylogenetic signal, so that they can be used to predict biomass for closely related tree species.

In this study, we use a comprehensive database compiled from 894 allometric biomass models published in 302 articles during 1980–2021 to examine whether parameters a and b of the model $W = aD^b$ exhibit phylogenetic signal for seed plants as a whole and for individual plant groups (e.g., gymnosperm trees versus angiosperm trees; evergreen trees versus deciduous trees; tropical trees versus temperate trees versus boreal trees). We also assess the relationship of difference in either model parameter with phylogenetic distance between pairwise tree species. Furthermore, allometric biomass model parameters may vary among sites with different environmental conditions; thus, the formability of parameters may be determined by a combination of environmental conditions and phylogeny. Accordingly, we also assess the relationship of difference in either model parameter with environmental distance between pairwise tree species.

2. Materials and methods

2.1. Data collection

We searched published articles employing a combination of the following search terms: “(tree biomass OR aboveground biomass OR plant biomass OR plant productivity) and (allometric biomass equation OR allometric model OR productivity model OR biomass equation OR biomass model)” through the Web of Science (<http://webofknowledge.com>), Google scholar (<http://scholar.google.com>), and the China National Knowledge Infrastructure (CNKI, <http://www.cnki.net>).

To avoid potential selection bias and duplicates, we cross-checked references of relevant articles published up to Dec 31, 2021 and subsequently selected eligible articles using the following criteria: (1) The biomass data must be obtained by harvesting and weighing based on setting the sample plot, with at least twenty sample trees on each site; therefore, articles without the measurements and using less than 20 sample trees per site were excluded. (2) The allometric biomass model must be built for aboveground biomass; thus, articles including models only for belowground biomass or only for the specific organ biomass of plants were excluded. (3) The form of the allometric biomass model is $W = aD^b$ or $\ln(W) = a + b\ln(D)$, where diameter at breast height (i.e., D) is the only independent variable of the model; consequently, articles with other variables and other types of models were excluded. (4) The specific species must be identified to build allometric models; thus, articles with unidentified species were excluded. (5) Data with a wide range of sample tree diameters were preferred for allometric biomass models of the same species at the same site. As a result, 302 articles were selected (Appendix A).

We compiled a database with 894 records from the 302 articles, including the following variables: (1) the location of the site of each allometric biomass model, including longitude and latitude; (2) allometric models, in the form of $W = aD^b$ and $\ln(W) = a + b\ln(D)$ including the parameters a and b ; (3) the number of sample trees used in model building; (4) taxonomic information of tree species corresponding to the model, including family, genus, and species; (5) climate data, including mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) of the tree species location; (6) soil organic carbon (SOC), which are among key factors determining tree species distributions (Kimmins, 2004).

Then, the collected data were standardized to facilitate analysis: (1) the allometric biomass models with the expression of $W = aD^b$ are uniformly transformed into the expression of $\ln(W) = a + b\ln(D)$; (2) the missing longitude and latitude data of the study site were obtained through the site name using Google Earth. Mean annual temperature and mean annual precipitation are considered as major constraints that determine the distributions of species over a broad spatial extent (Weigelt et al., 2015; Patrick and Stevens, 2016). We obtained values for two key climate variables from the CHELSA database (<http://chelsea-climate.org/>; corresponding to bio1 and bio12, respectively). The missing soil data was derived from the soil profile data of the Regrided Harmonized World Soil Database v.1.21 (Wieder, 2014).

Botanical nomenclature were standardized according to World Plants (<https://www.worldplants.de>), using the package U.Taxonstand (Zhang and Qian, 2023), and our final dataset included 276 species in 59 families and 123 genera. We divided the tree species into two taxonomic groups (gymnosperm and angiosperm), two leaf duration groups (evergreen and deciduous), and three climate groups (tropical, temperate and boreal). To classify the tree species into the three climate groups, we documented the global distribution of each species based on the information on the Plants of the World Online (www.plantsoftheworldonline.org), and calculated the mean values of the mean annual temperature based on the CHELSA climate database, and considered a species being tropical if its average of mean annual temperature >20 °C, temperate if its average of mean annual temperature being <20 °C and >5 °C, or boreal if its average of mean annual temperature being <5 °C (Ricklefs, 2008).

2.2. Data analysis

All phylogenetic analyses based on model parameters took place in the R environment (Ihaka and Gentleman, 1996; Pagel, 1999; Jin

and Qian, 2022). Firstly, we used the V.PhyloMaker2 package (Jin and Qian, 2022) to generate a phylogenetic tree for the species in our database as a reference for phylogenetic analysis (Molina-Venegas and Rodríguez, 2017). Secondly, whether allometric biomass model parameters a and b are phylogenetically constrained was assessed using both Pagel's λ and Blomberg K statistics (Pagel, 1999; Blomberg et al., 2003). These two indices are commonly used to assess phylogenetic signal of a focal trait with respect to a phylogeny (Qian and Zhang, 2014). For both indices, a value of zero indicates a random distribution of a trait with respect to the phylogeny whereas a value of one indicates that the evolution of the trait matches expectations under the Brownian motion model of evolution (Qian and Zhang, 2014). Heteroscedastic biomass model parameters a and b are compared on the same phylogenetic tree, reflecting their variation affected by interspecific relationships as they evolve over time (Raamsdonk et al., 2001; Butler and King, 2004). We used the function *phylosig* from phytools to calculate the λ and K metrics (Kembel et al., 2010; Jin and Qian, 2022). The statistical significance of Pagel's λ was determined by comparing the likelihood of the observed λ value with the likelihood of a model that assumes complete phylogenetic independence (Felsenstein, 1985; Pagel, 1999; Münkemüller et al., 2012). The statistical significance of Blomberg's K was determined by comparing Blomberg's K and the null model. Phylogenetic signal was considered significant ($p < 0.05$) when the observed value was greater than the null model value derived from 1000 randomizations.

With the pairwise approach, we explored how phylogenetic distance (dissimilarity) was related to environmental distance

between sites. The 894 data in our dataset would result in 799,236 pairs of data. The environmental distance between each pair of sites was measured as the Euclidean distance between the sites. The parameter distance between each pair of sites was measured as the absolute value of the difference of values of parameter a or b between the sites. We used simple regression analysis to examine the relationship between parameter a or b and phylogenetic or environmental distance.

3. Results and discussion

The analyses of Blomberg's K and Pagel's λ showed that parameters a and b of allometric biomass models were not phylogenetically constrained for all tree species as a whole and for different groups of species (Table 1). When all species were considered, values of Blomberg's K and Pagel's λ tended to converge to 0, and were not significant ($p > 0.05$ in all cases; Table 1). Our study suggested that the allometric biomass model parameters that we investigated were not to be more similar among more closely related species than among more distantly related species, which suggested that differences in model parameters examined in this study were not driven by evolutionary processes. When species in different groups were analyzed separately, our study showed that there were no significant phylogenetic signals in all groups of plants (Table 1).

The results of regression analysis showed no significant relationships of difference of parameter a or b with phylogenetic and environmental distances, with nearly all values of R^2 being less than 0.01, even though some relationships were statistically significant

Table 1

Phylogenetic signal of parameters a and b for different groups of tree species. Abbreviations in the first column: D = deciduous, E = evergreen, A = angiosperm, and G = gymnosperm.

Plant group	No. of species	Parameter a				Parameter b			
		Blomberg's K		Pagel's λ		Blomberg's K		Pagel's λ	
		K	p-value	Λ	p-value	K	p-value	λ	p-value
All species	276	0.041	0.026	<0.001	1.000	0.053	0.001	<0.001	1.000
Gymnosperms	61	0.038	0.089	0.047	0.906	0.035	0.122	0.187	0.102
Angiosperms	215	0.085	0.283	<0.001	1.000	0.120	0.037	<0.001	1.000
Angiosperms (D)	107	0.101	0.119	<0.001	1.000	0.114	0.052	<0.001	1.000
Angiosperms (E)	63	0.031	0.735	<0.001	1.000	0.120	0.250	<0.001	1.000
Boreal (A)	8	0.137	0.702	<0.001	1.000	0.023	0.991	<0.001	1.000
Temperate (A)	98	0.080	0.154	0.586	0.221	0.128	0.010	0.064	0.683
Tropical (A)	109	0.102	0.785	<0.001	1.000	0.148	0.505	<0.001	1.000
Boreal (G)	6	0.098	0.832	<0.001	1.000	0.107	0.832	<0.001	1.000
Temperate (G)	42	0.052	0.166	<0.001	1.000	0.045	0.264	<0.001	1.000
Tropical (G)	13	0.030	0.221	<0.001	1.000	0.033	0.175	0.436	0.260

Table 2

Coefficient of determination (R^2) and p-value for regressions of parameter a or b on either phylogenetic distance or environmental distance for different groups of tree species. Abbreviations in the first column: D = deciduous, E = evergreen, A = angiosperm, and G = gymnosperm. N = the number of pairwise sites.

Plant group	N	Parameter a				Parameter b			
		Phylo.dist		Env.dist		Phylo.dist		Env.dist	
		R^2	p-value	R^2	p-value	R^2	p-value	R^2	p-value
All species	399,171	<0.001	0.024	<0.001	0.395	<0.001	0.003	0.001	0.141
Gymnosperms	71,253	0.003	0.081	0.002	0.157	0.004	0.058	<0.001	0.826
Angiosperms	132,870	0.001	0.053	<0.001	0.838	0.002	0.004	0.002	0.086
Angiosperms (D)	47,895	0.001	0.250	0.001	0.434	0.004	0.002	0.002	0.250
Angiosperms (E)	10,585	0.001	0.282	0.001	0.630	0.002	0.282	0.001	0.551
Boreal (A)	528	<0.001	0.732	0.003	0.575	0.001	0.603	<0.001	0.988
Temperate (A)	44,253	0.001	0.160	<0.001	0.731	<0.001	0.336	0.004	0.095
Tropical (A)	17,020	<0.001	0.505	0.001	0.454	<0.001	0.730	<0.001	0.701
Boreal (G)	4371	<0.001	0.559	<0.001	0.997	0.001	0.282	0.006	0.199
Temperate (G)	32,385	0.006	0.028	<0.001	0.649	0.006	0.040	0.002	0.194
Tropical (G)	406	0.019	0.232	0.015	0.223	<0.001	0.905	0.008	0.362

($p < 0.05$) or marginally significant ($p < 0.10$) (Table 2). Our analyses suggest that model parameters a and b were neither phylogenetically constrained nor modulated by environmental factors, regardless of whether all tree species were considered or species in different groups were considered. Genetic legacy effects are considered as a product of long-term evolutionary processes (represented by phylogeny), during which species adapt to shifts in abiotic and biotic stressors, caused by climate, soil and interactions with other species (Losos, 2008). Phylogeny includes ancient adaptation and differentiation from other clades, whereas species include more genetic and epigenetic factors which, through evolutionary convergence or divergence, can generate similar or different morphological and functional characteristics. It can be understood that different species evolved to produce similar or different tree sizes, and this variability may be expressed as differences in model biomass.

The insignificant phylogenetic signal of the allometric biomass model parameters measured in all species suggests that phylogeny is not a factor limiting the distribution of model parameters, indicating that the limitation is not present among gymnosperms or angiosperms in different climatic regions. The diameter at breast height (DBH) and model parameters are two key factors in predicting biomass (in allometric biomass models of our study). DBH has been shown to be phylogenetically limited in previous studies (Maynard et al., 2022), while it was confirmed that parameters are not phylogenetically limited in this study. We infer that there is no cascade effect of phylogenetic limitation in predicting aboveground biomass. This result disproves our hypothesis that the allometric biomass model parameters are phylogenetically constrained. The genealogical information of species cannot be used to predict biomass for closely related species. However, due to limitation of data, our study did not consider many ecological factors that can affect variation of model parameters (e.g., aspect and slope of sites, microhabitat). Future studies exploring the relationships between model parameters and phylogenetic signal and distance may include more ecological factors.

It has been shown that independent variables of biomass models such as tree size had significant phylogenetic signals (de Aguiar-Campos et al., 2021). McCullough and O'Brien (2022) compared the allometric slopes of intra-sexually-selected structures and found they are regulated by biological evolutionary processes. Similarly, Palaoro et al. (2022) found that the allometric parameters of contest-related traits could be predicted in tusked harvestmen (*Phareicranus manauara*) using evolutionary constraints on allometric slopes. The allometric slopes (parameter b) are more ecologically relevant than the intercept (parameter a) and have received more attention (Tomkins et al., 2005). For parameter b, it is believed that there are phylogenetic limitations in other allometric biomass models, such as $\ln(W) = a + b\ln(D^2H)$ and $\ln(W) = a + b\ln(\rho D^2H)$, where W, D, H and ρ represent aboveground biomass, diameter at breast height, height and wood density, respectively (Chave et al., 2005). Previous studies have used other models to predict aboveground biomass of trees (e.g., Nizamani et al., 2021), but the number of such studies is not large enough for a robust synthesis analysis.

At present, the fraction of global plant biomass occurring belowground as roots is poorly understood. The establishment of the allometric biomass equation in the belowground fraction was much less than that in the aboveground fraction. Root-to-crown ratio, an allometric growth relationship between aboveground and belowground biomass, may be phylogenetic limited (Ma et al., 2021).

The phylogenetic constraints of the parameters are not considered in any of various global models that estimate forest carbon by far. There are still many types of equations in the studies of

predicting biomass where phylogenetic and environmental constraints may exist, providing us ideas and directions for further research. Future studies should investigate whether parameters of other biomass models are influenced by phylogenetic and environmental factors in order for models to more accurately predict biomass for those species that do not have parameterized biomass models.

4. Conclusion

Our study showed that phylogeny does not modulate parameter distribution patterns in allometric models of aboveground biomass for trees. This finding holds true for both gymnosperm and angiosperm trees, for both evergreen and deciduous trees, and for trees in different climate conditions (tropical, temperate and boreal). Although the phylogenetic constraint is not a significant driver of parameter variation for the model parameters examined here, future study should investigate whether parameters for other variables of a biomass model (i.e. other than W and D) or other types of model have phylogenetic signal.

Author contributions

X.H. and H.Q. designed the study. Z.W. and F.L. collected the data. F.L. and Y.J. analyzed the data. All authors contributed significantly to the writing of the manuscript.

Declaration of competing interest

The author declares no conflict of interest.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.pld.2022.11.005>.

References

- Blomberg, S.P., Garland Jr., T., Ives, A.R., 2003. Testing for phylogenetic signal in comparative data, behavioral traits are more labile. *Evolution* 57, 717–745.
- Brown, J.H., Gillooly, J.F., Allen, A.P., et al., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Butler, M.A., King, A.A., 2004. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* 164, 683–695.
- Cavender-Bares, J., Ackerly, D.D., Baum, D.A., et al., 2004. Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.* 163, 823–843.
- Chave, J., Andalo, C., Brown, S., et al., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99.
- Chazdon, R.L., Careaga, S., Webb, C., et al., 2003. Community and phylogenetic structure of reproductive traits of woody species in wet tropical forests. *Ecol. Monogr.* 73, 331–348.
- Damuth, J., 2001. Scaling of growth: plants and animals are not so different. *Proc. Natl. Acad. Sci. U.S.A.* 98, 2113–2114.
- de Aguiar-Campos, N., Coelho de Souza, F., Maia, V.A., et al., 2021. Evolutionary constraints on tree size and above-ground biomass in tropical dry forests. *J. Ecol.* 109, 1690–1702.
- Desclaves, Y., Morand, S., Legendre, P., 2002. Evolution and determinants of host specificity in the genus *Lamellodiscus* (Monogenea). *Biol. J. Linn. Soc.* 77, 431–443.
- Felsenstein, J., 1985. Phylogenies and the comparative method. *Am. Nat.* 125, 1–15.
- Gilbert, G.S., Webb, C.O., 2007. Phylogenetic signal in plant pathogen–host range. *Proc. Natl. Acad. Sci. U.S.A.* 104, 4979–4983.
- Helmus, M.R., Savage, K., Diebel, M.W., et al., 2007. Separating the determinants of phylogenetic community structure. *Ecol. Lett.* 10, 917–925.

- Ihaka, R., Gentleman, R., 1996. R: a language for data analysis and graphics. *J. Comput. Graph Stat.* 5, 299–314.
- Jin, Y., Qian, H., 2022. VPhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Divers.* 44, 335–339.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., et al., 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464.
- Kimmins, J.P., 2004. *Forest Ecology*, Third ed. Prentice-Hall, Upper Saddle River, New Jersey.
- Losos, J.B., 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* 11, 995–1003.
- Ma, H., Mo, L., Crowther, T.W., et al., 2021. The global distribution and environmental drivers of aboveground versus belowground plant biomass. *Nat. Ecol. Evol.* 5, 1110–1122.
- Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., et al., 2022. Global relationships in tree functional traits. *Nat. Commun.* 13, 1–12.
- McCullough, E.L., O'Brien, D.M., 2022. Variation in allometry along the weapon-signal continuum. *Evol. Ecol.* 36, 591–604.
- Molina-Venegas, R., Rodríguez, M.A., 2017. Revisiting phylogenetic signal; strong or negligible impacts of polytomies and branch length information? *BMC Evol. Biol.* 17, 53.
- Münkemüller, T., Lavergne, S., Bzeznik, B., et al., 2012. How to measure and test phylogenetic signal. *Methods Ecol. Evol.* 3, 743–756.
- Nizamani, M.M., Harris, A.J., Cheng, X.L., et al., 2021. Positive relationships among aboveground biomass, tree species diversity, and urban greening management in tropical coastal city of Haikou. *Ecol. Evol.* 11, 12204–12219.
- Pagel, M., 1999. Inferring the historical patterns of biological evolution. *Nature* 401, 877–884.
- Palaoro, A.V., García-Hernández, S., Buzatto, B.A., et al., 2022. Function predicts the allometry of contest-related traits, but not sexual or male dimorphism in the amazonian tusked harvestman. *Evol. Ecol.* 36, 605–630.
- Pantin, C.F.A., 1932. Problems of relative growth. *Nature* 129, 775–777.
- Patrick, L.E., Stevens, R.D., 2016. Phylogenetic community structure of North American desert bats: influence of environment at multiple spatial and taxonomic scales. *J. Anim. Ecol.* 85, 1118–1130.
- Prinzing, A., Durka, W., Klotz, S., et al., 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 268, 2383–2389.
- Qian, H., Deng, T., Sun, H., 2019. Global and regional tree species diversity. *J. Plant Ecol.* 12, 210–215.
- Qian, H., Zhang, J., 2014. Using an updated time-calibrated family-level phylogeny of seed plants to test for non-random patterns of life forms across the phylogeny. *J. Syst. Evol.* 52, 423–430.
- Raamsdonk, L.M., Teusink, B., Broadhurst, D., et al., 2001. A functional genomics strategy that uses metabolome data to reveal the phenotype of silent mutations. *Nat. Biotechnol.* 19, 45–50.
- Ricklefs, R.E., 2008. *The Economy of Nature*. W. H. Freeman.
- Silvertown, J., Dodd, M., Gowing, D., et al., 2006a. Phylogeny and the hierarchical organization of plant diversity. *Ecology* 87, S39–S49.
- Silvertown, J., McConway, K., Gowing, D., et al., 2006b. Absence of phylogenetic signal in the niche structure of meadow plant communities. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 273, 39–44.
- Tomkins, Joseph L., Kotiaho, Janne S., LeBas, Natasha R., 2005. Matters of scale: positive allometry and the evolution of male dimorphisms. *Am. Nat.* 165, 389–402.
- Vitt, L.J., Pianka, E.R., 2005. Deep history impacts present-day ecology and biodiversity. *Proc. Natl. Acad. Sci. U.S.A.* 102, 7877–7881.
- Vitt, L.J., Zani, P.A., Espósito, M.C., 1999. Historical ecology of Amazonian lizards: implications for community ecology. *Oikos* 87, 286–294.
- Webb, C.O., Gilbert, G.S., Donoghue, M.J., 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology* 87, S123–S131.
- Weiblen, G.D., Webb, C.O., Novotny, V., et al., 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology* 87, S62–S75.
- Weigelt, P., Daniel Kissling, W., Kisel, Y., et al., 2015. Global patterns and drivers of phylogenetic structure in island floras. *Sci. Rep.* 5, 12213.
- Wieder, W., 2014. *Regridded Harmonized World Soil Database v1.2*. ORNL Distributed Active Archive Center.
- Wiens, J.J., Graham, C.H., Moen, D.S., et al., 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *Am. Nat.* 168, 579–596.
- Zhang, J., Qian, H., 2023. U.Taxonstand: an R package for standardizing scientific names of plants and animals. *Plant Divers.* 45, 1–5.