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Corrigendum (Russo et al. 2007): A Re-Analysis of Growth–Size Scaling Relationships of Woody Plant Species

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*Corrigendum***(Russo et al. 2007): A Re-Analysis of Growth–Size Scaling Relationships of Woody Plant Species**

Russo et al. (2007) tested two predictions of the Metabolic Ecology Model (Enquist et al. 1999, 2000) using a data set of 56 tree species in New Zealand: (i) the rate of growth in tree diameter (dD/dt) should be related to tree diameter (D) as $dD/dt = \beta D^\alpha$ and (ii) tree height (H) should scale with tree diameter as $H(D) = \gamma D^\delta$, where t is time, β and γ are scaling coefficients that may vary between species, and α and δ are invariant scaling exponents predicted to equal 1/3 and 2/3, respectively (Enquist et al. 1999, 2000). To this end, Russo et al. (2007) used maximum likelihood methods to estimate α and δ and their two-unit likelihood support intervals. As noted in our original manuscript, the growth–diameter scaling exponent and coefficient covary, complicating the estimation of confidence intervals. We now recognize that the method we used to estimate support intervals (using marginal support intervals with the nu-

sance parameters fixed) underestimates the breadth of the interval and that the support intervals, properly estimated, should account for the variability in all parameters (Hilborn & Mangel 1997). This can be done in several ways. For example, the Hessian matrix can be used to estimate the standard deviation for each parameter, assuming asymptotic normality. Alternatively, one can systematically vary the parameter for which the interval is being estimated, re-estimate the Maximum likelihood estimates (MLEs) for the other parameters, and take the support interval to be the values of the target parameter that result in log likelihoods that are two units away from the maximum (Edwards 1992; Hilborn & Mangel 1997). A third and more direct approach to comparing data with prediction is to use the likelihood ratio test (LRT), which explicitly tests if a model with a greater number of parameters provides a significantly better fit

Table 1. Results of likelihood ratio tests (LRTs) indicating the numbers of New Zealand tree species for which a model in which the scaling exponent (α for the growth–diameter scaling model or δ for the height–diameter scaling model) was estimated was significantly more likely than a model with the exponent fixed at the value predicted by the Metabolic Ecology Model ('model with exponent estimated was more likely'), the numbers of species for which this was not the case ('model with exponent fixed at predicted value was more likely'), and the total numbers of species tested ('total tested').

	Total tested	Model with exponent estimated was more likely	Model with exponent fixed at predicted value was more likely
<i>Growth–diameter scaling exponent prediction: $\alpha = 1/3$</i>			
All stems			
Canopy trees	18	11	7
Small trees	25	8	17
Shrubs	13	1	12
Total	56	20	36
Stems 3–20 cm			
Canopy trees	14	8	6
Small trees	24	11	13
Shrubs	13	3	10
Total	51	22	29
Stems ≥ 20 cm			
Canopy trees	11	5	6
Small trees	3	1	2
Shrubs	–	–	–
Total	14	6	8
<i>Height–diameter scaling exponent prediction: $\delta = 2/3$</i>			
Canopy trees	18	17	1
Small trees	17	14	3
Shrubs	6	2	4
Total	41	33	8

For the LRTs, statistical significance was assessed based on the chi-squared distribution with a single degree of freedom at $P = 0.05$. Counts of species are categorized according to growth form and size class. A dash indicates that there were no species in this category with sufficient sample size to test.

to the data than a simpler model in which some parameters are fixed at predicted values (Hilborn & Mangel 1997; Bolker in press).

Here, we re-analyze our data using LRTs, present a table revising Tables 1 and 2 from Russo et al. (2007), and reevaluate whether there is statistical support for the predictions of the Metabolic Ecology Model that we tested in Russo et al. (2007). We used LRTs to test, respectively, whether a model in which α , or δ , was estimated at its MLE had a significantly greater likelihood than did a model with $\alpha = 1/3$, or $\delta = 2/3$, for the growth-diameter and height-diameter scaling relationships.

For the growth-diameter scaling exponent, in analyses across all species for all stems, small stems (3–20 cm) and large stems (≥ 20 cm), in all three cases, the model in which α was estimated was significantly more likely than the model with $\alpha = 1/3$ (all stems: $\chi^2 = 460.693$, $P < 0.001$; small stems: $\chi^2 = 201.530$, $P < 0.001$; large stems: $\chi^2 = 28.892$, $P < 0.001$), providing no support for this prediction of the Metabolic Ecology Model. In species-specific analyses of stems of all sizes, for 20 of 56 tree species, the model in which α was estimated was significantly more likely than the model with α fixed at $1/3$ (Table 1). In species-specific analyses of small and large stems, for 22 of 51 and six of 14 tree species, respectively, the model in which α was estimated was significantly more likely than the model with α fixed at $1/3$ (Table 1). For the height-diameter scaling relationship, for 33 of 41 tree species, the model in which δ was estimated was significantly more likely than the model in which δ was fixed at $2/3$ (Table 1).

These re-analyses support our original conclusions in that (i) the exponents of the growth-diameter and height-diameter scaling relationships are not invariant among species or among growth forms, (ii) the combined data across all species provide no support for the predicted growth-diameter scaling exponent and (iii) in analyses by species, there was little support for the predicted height-diameter scaling exponent. Results of analyses of the growth-diameter scaling exponent by species were mixed: there was consistent variation among growth forms in the extent to which the predicted exponent was supported in the scaling model comparisons, with canopy trees showing little support, smaller trees showing mixed support and shrubs showing greater support for the predicted values. This is likely due in part to the extent to which access to and allocation of resources changes with size for different growth forms, as noted in Russo et al. (2007). It is also

important to point out that the highly variable nature of tree growth, which is influenced by many endogenous and exogenous factors in addition to tree size and temperature (Weiner & Thomas 2001; Clark et al. 2003; King et al. 2005), combined with the strong covariation between model parameters, make the tree growth-diameter scaling exponent difficult to estimate.

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References

- Bolker, B. (in press). *Ecological Models and Data in R*. Princeton University Press, Princeton, N.J., U.S.A.
- Clark, J.S., J. Mohan, M. Dietze, and I. Ibanez (2003). Coexistence: how to identify trophic trade-offs. *Ecology* 84: 17–31.
- Edwards, A.W.F. (1992). *Likelihood*, expanded edition. Johns Hopkins University Press, Baltimore, Md., U.S.A.
- Enquist, B.J., G.B. West, E.L. Charnov, and J.H. Brown (1999). Allometric scaling of production and life-history variation in vascular plants. *Nature* 401: 907–911.
- Enquist, B.J., G.B. West, and J.H. Brown (2000). Quarter-power allometric scaling in vascular plants: functional basis and ecological consequences. In: *Scaling in Biology* (eds. J.H. Brown and G.B. West). Oxford University Press, New York, U.S.A., pp. 167–198.
- Hilborn, R., and M. Mangel (1997). *The Ecological Detective*. Princeton University Press, Princeton, N.J., U.S.A.
- King, D.A., S.J. Davies, M.N. Nur Supardi, and S. Tan (2005). Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional Ecology* 19: 445–453.
- Russo, S.E., S.K. Wiser, and D.A. Coomes (2007). Growth-size scaling relationships of woody plant species differ from predictions of the Metabolic Ecology Model. *Ecology Letters* 10: 889–901.
- Weiner, J., and S.C. Thomas (2001). The nature of tree growth and the 'age-related decline in forest productivity.' *OIKOS* 94: 374–376.