

1   **Running head:** Temporal dynamics across a gradient

2

3   **Title:** Deconstructing the signal: phylogenetic structure, elevation change and the implications for  
4   species coexistence

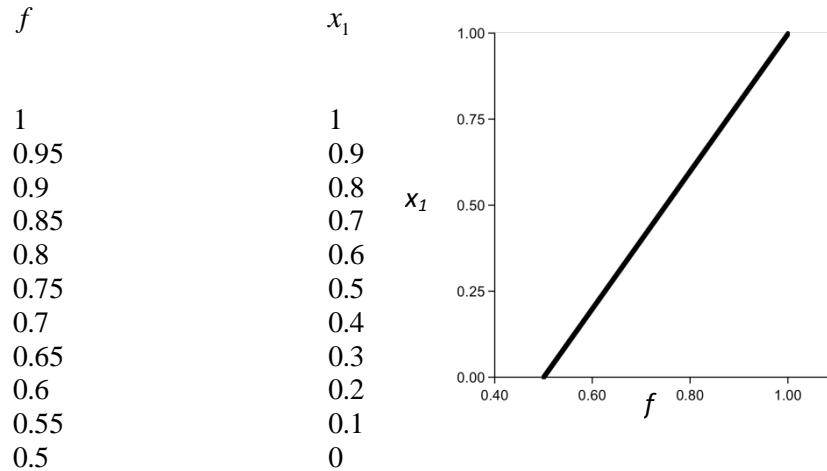
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There is another way to have species 1 dominant, even overwhelmingly so, in the balmy uplands, yet the rarer close to sea level. Take the advantage parameter  $a$  as fixed and vary the fraction of good years  $f$ . At higher elevations  $f$  can be equal to 1 and decrease as we go down hill. Numbers are given in table 2 below and portrayed in the adjacent figure:

Table 2.  $a=2.0$  Original model with  $f$  decreasing

This is reasonable enough, in that species 1 is as dominant as desired at high elevations and has become the rarer as the fraction of good years  $f$  drops with descending altitude to a value of about 0.7. We would suppose that is about Chamela altitude. The uncomfortable thing about it is that the fraction of good years decreases at lower elevations (in table 2 above the advantage factor is independent of elevation at a value of 2). If the advantage factor  $a$  grew with increasing harshness, then the fraction  $x_1$  would drop less rapidly with  $f$ .

There is in fact a way of varying  $x_1$  over the full range from 1 at high elevations to values typical of Chamela without varying either the fraction of good years  $f$  or the advantage of species 1 over species 2 during good years. In the original model it was supposed that during bad years species 1 could not recruit at all, that is the advantage parameter in bad years is zero. If this assumption is relaxed so that in bad years species 1 is at a competitive disadvantage (that is, the parameter  $a < 1$ ) then the full range is covered for  $f$  considerably less than 1. In this development of the original model the variation of  $x_1$  can be assigned to variation of its degree of disadvantage as conditions get harsher. For the fraction  $f$  the advantage of species 1 is  $a^+$  ( $> 1$ ) and for  $1-f$  the advantage parameter is  $a^-$  ( $< 1$ ). I solved the lottery equations for this extended model back in 2003 or 04 – the analytic solution is more complicated than the solution for the original model.

The extended two-component lottery model has an analytic solution valid under the same conditions as the original. The model differs from the original only in that the more sensitive species is able to recruit during bad times. The fraction of good times is  $f$  and during these times, the more sensitive species has the advantage  $a^+$  over the slow but steady species. In bad times, the advantage factor is  $a^-$  (less than 1). Then the population fraction  $x_1$  of the sensitive species is given by the expression

$$x_1 = \frac{(1-a^-/a^+)f - (1/a^+ - a^-/a^+)}{(a^+-1)\{1/a^+ - a^-/a^+\}}$$

The formula could be written in various ways, but this best suits its current use. Figure 1S below serves as an illustration of this more complex model.

**Figure 1S. Changing relative abundance in the complex lottery model.** In this figure  $x_1$  = the proportional abundance of the more sensitive species 1,  $f$  = the frequency of good years and  $a^+$  represent the relative competitive advantage of species 1 over the less sensitive species 2.

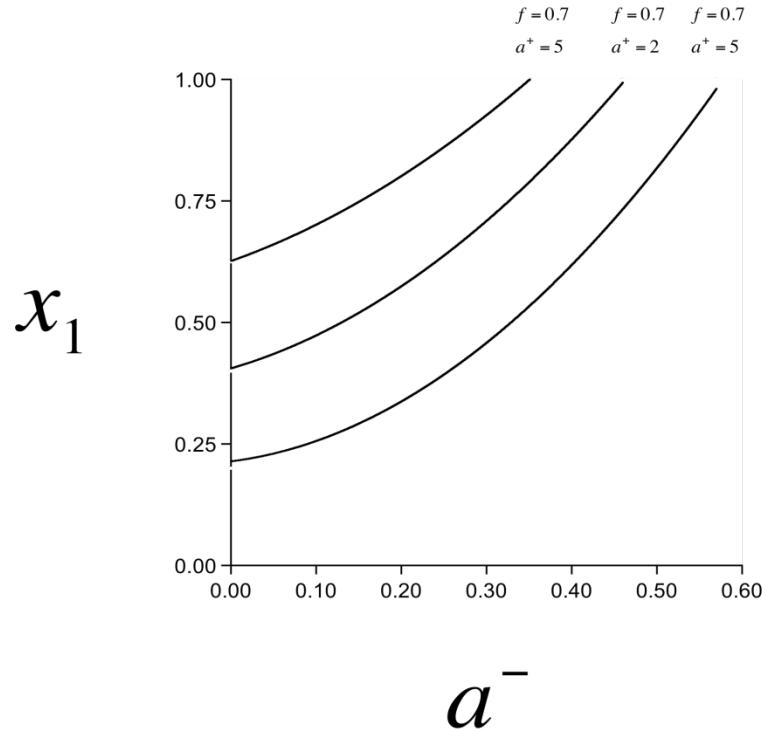
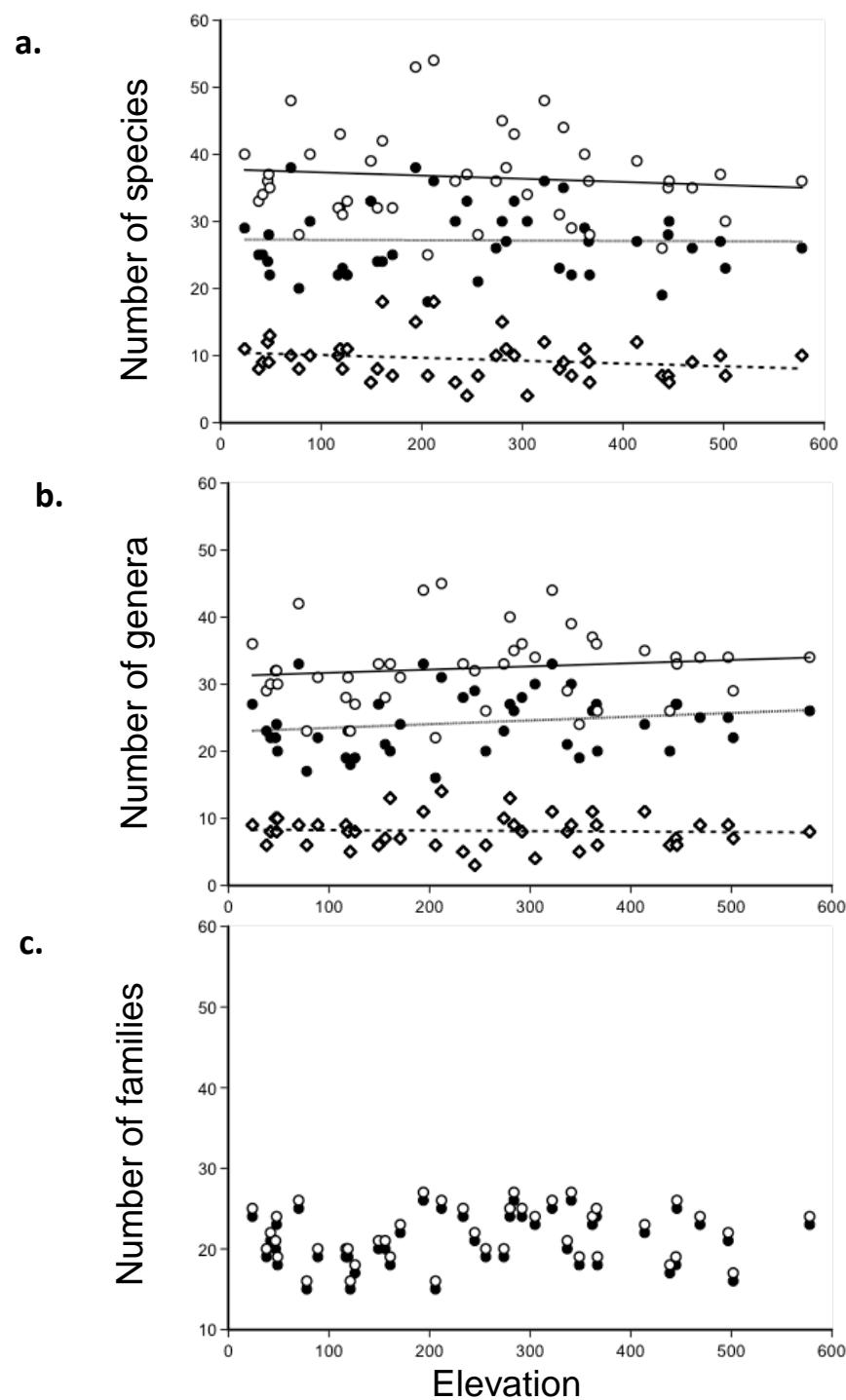


Figure 1S shows that it is perfectly possible to have the same time structure in environmental conditions at all elevations, maintain the Chamaela results at Chamaela elevations and yet have the more sensitive species as dominant as desired at the highest (most benign) elevations, even though in hard times it is at a significant disadvantage relative to the more tolerant species.

Obviously, some mixture of these effects here treated individually could be constructed to match exactly output with observation, but the point here is general agreement with expectations, with further development of the theory in a more appropriate treatment dedicated to it specifically. The essential point is that the time structured lottery model can account for the more competitive of a pair of congeneric species being very dominant high up where the environment is less water-stressed, and yet the rarer at sea level, the hottest and driest environment.

**Appendix B. General patterns of taxa distribution relative to elevation.**

**Figure 1. Number of taxa by elevation.** a. Number of species in the full tree (hollow circles) and in the non-Fabaceae (filled circles) and Fabaceae (hollow diamonds) subtrees. b. Number of genera in each of the three trees. c. Number of families in the full and non-Fabaceae trees. Solid line = full tree; fine dashed line = non-Fabaceae tree; coarse dashed line = Fabaceae. See following table for regression equations. Salient points are that all three trees show no significant change in taxa numbers across elevation (Figs. 1a & b) and that the Fabaceae occurs in all plots (Fig 1c).

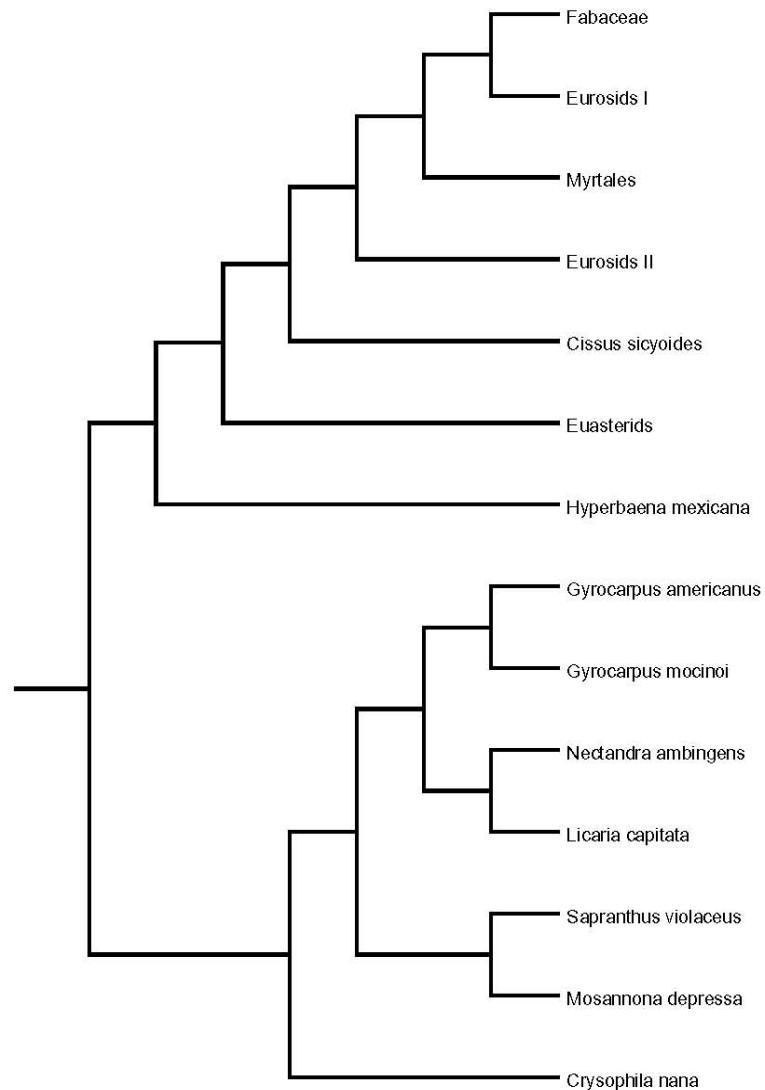


**Table 1.** Regression equations of taxon numbers relative to elevation.

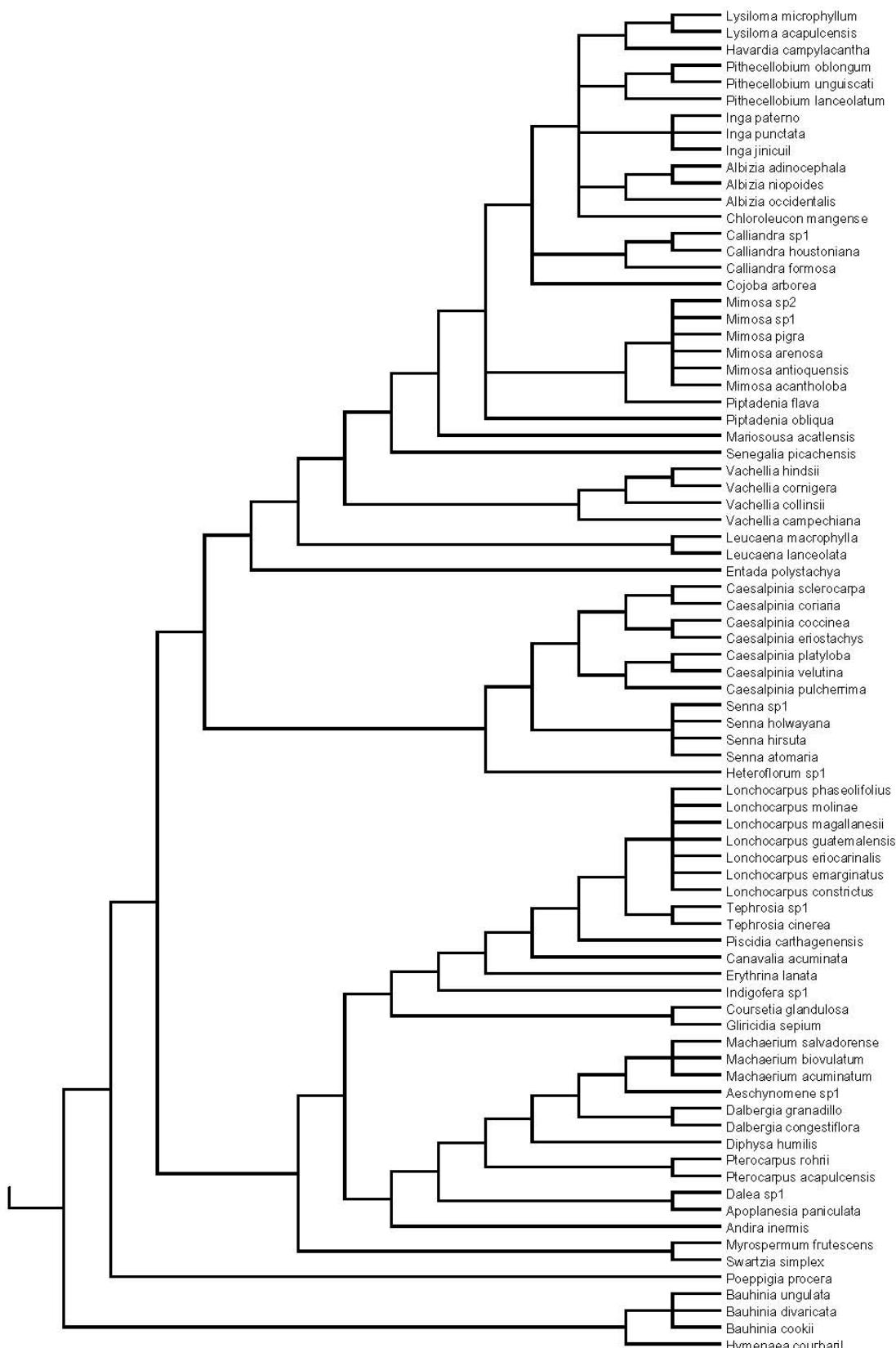
Elevation vs	Full tree	Fabaceae	Non-Fabaceae
<b>Number of species</b>	= 37.771 – 0.005m p = 0.495	= 10.48 – 0.004m p = 0.195	= 27.291 – 0.001m p = 0.922
<b>Number of genera</b>	= 31.196 + 0.005m p = 0.402	= 8.291 – 0.001m p = 0.779	= 22.905 + 0.006m p = 0.225
<b>Number of families</b>	= 21.081 + 0.003m p = 0.321	NA	= 20.081 + 0.003m p = 0.321

**Appendix C. Phylogenetic tree of Oaxacan tropical dry forest (TDF) trees**

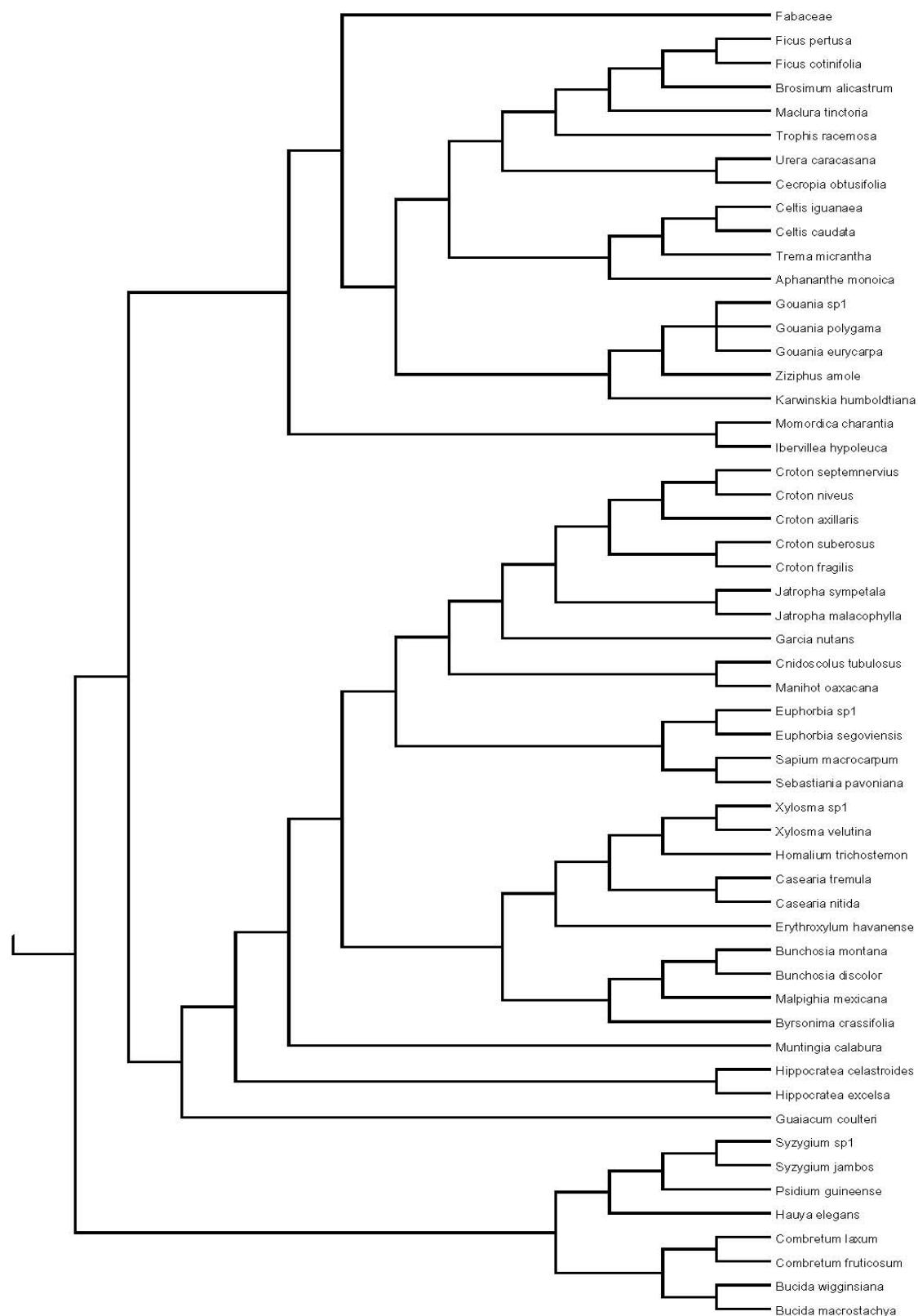
Oaxaca TDF Phylogeny – Backbone



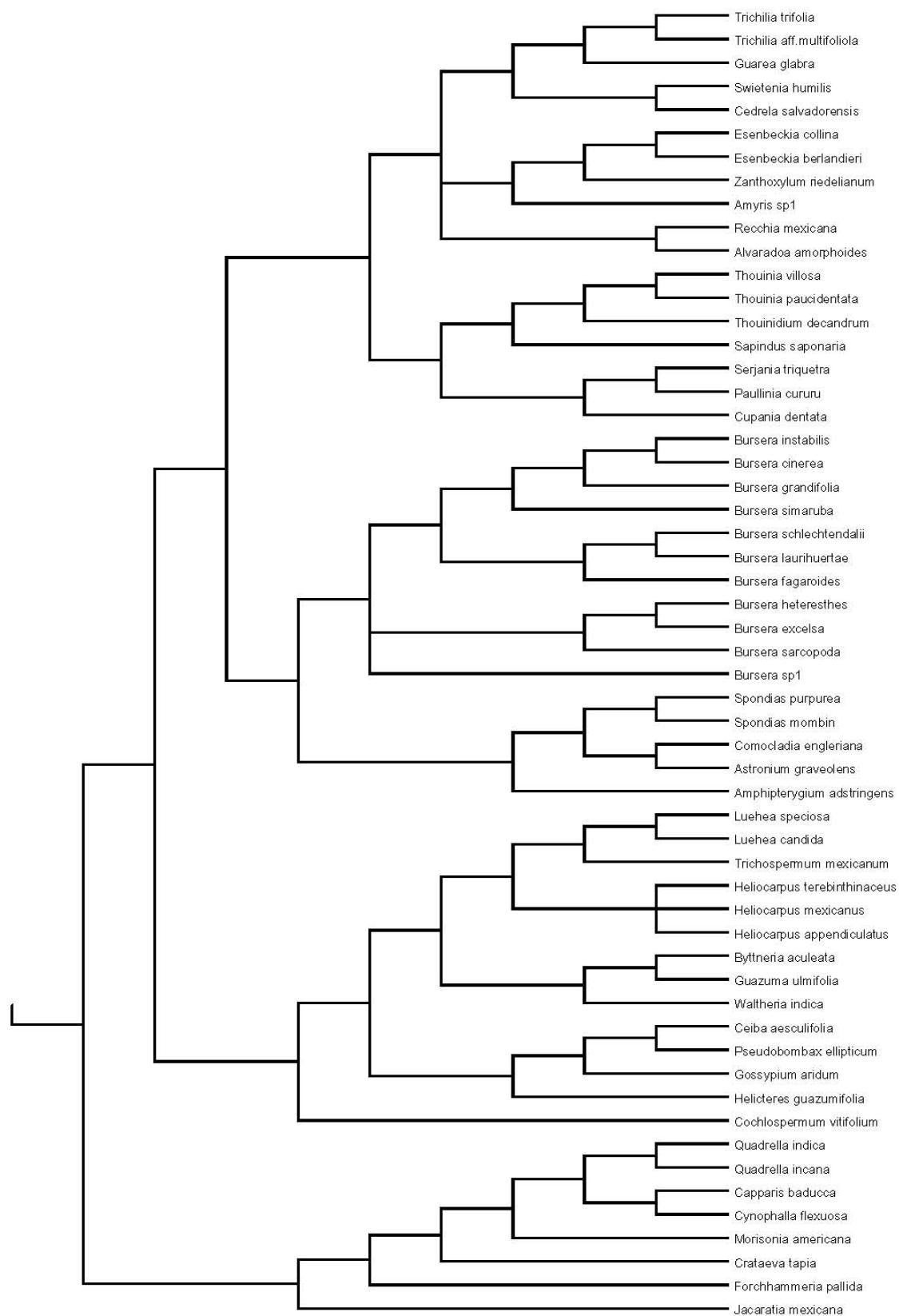
## Oaxaca TDF Phylogeny - Fabaceae



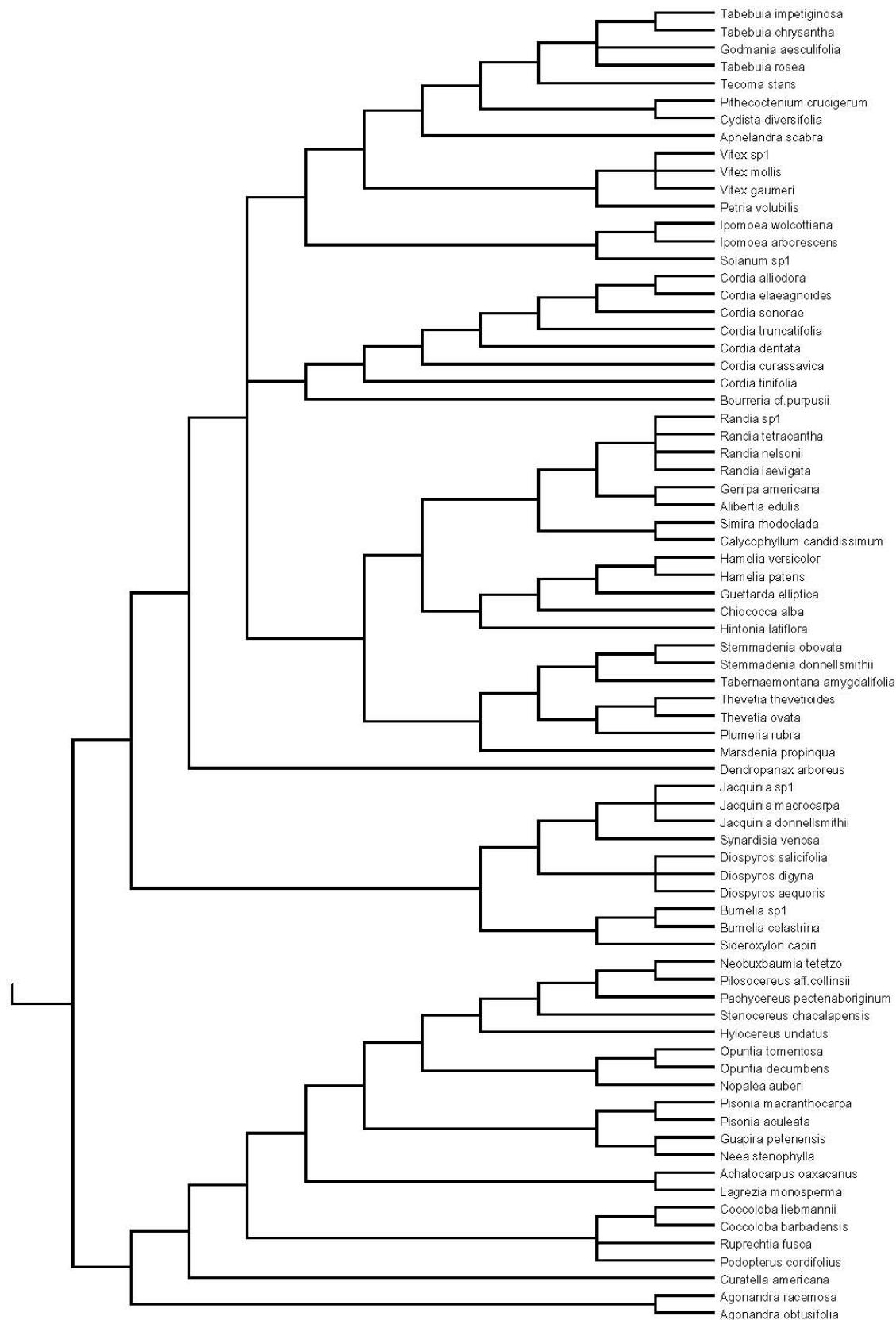
## Oaxaca TDF Phylogeny – Eurosids I and Mytales without Fabaceae



## Oaxaca TDF Phylogeny – Eurosids II



## Oaxaca TDF Phylogeny – Euasterids



## References:

- Aguilar-Ortigoza, C. J. and V. Sosa. 2004. The evolution of toxic phenolic compounds in a group of Anacardiaceae genera. *Taxon* 53:357-364.
- Alverson, W. S., B. A. Whitlock, R. Nyffeler, C. Bayer, and D. A. Baum. 1999. Phylogeny of the core Malvales: Evidence from *ndhF* sequence data. *American Journal of Botany* 86:1474-1486.
- Arias, S., T. Terrazas, H. J. Arreola-Nava, M. Vazquez-Sanchez, and K. M. Cameron. 2005. Phylogenetic relationships in *Peniocereus* (Cactaceae) inferred from plastid DNA sequence data. *Journal of Plant Research* 118:317-328.
- Arias, S., T. Terrazas, and K. Cameron. 2003. Phylogenetic analysis of *Pachycereus* (Cactaceae, Pachycereeae) based on chloroplast and nuclear DNA sequences. *Systematic Botany* 28:547-557.
- Barneby, R. C. and J. W. Grimes. 1996. Silk tree, guanacaste, monkey's earring: A generic system for the Synandrous Mimosaceae of the Americas: Part I. *Abarema*, *Albizia*, and allies. *Memoirs of the New York Botanical Garden* 74:1-292.
- Barneby, R. C. and J. W. Grimes. 1997. Silk tree, guanacaste, monkey's earring: A generic system for the Synandrous Mimosaceae of the Americas: Part II. *Pithecellobium*, *Cojoba*, and *Zygia*. *Memoirs of the New York Botanical Garden* 74:1-149.
- Baum, D. A., S. D. Smith, A. Yen, W. S. Alverson, R. Nyffeler, B. A. Whitlock, and R. L. Oldham. 2004. Phylogenetic relationships of Malvatheca (Bombacoideae and Malvoideae; Malvaceae Sensu Lato) as inferred from plastid DNA sequences. *American Journal of Botany* 91:1863-1871.
- Becerra, J. X. and D. L. Venable. 1999. Nuclear ribosomal DNA phylogeny and its implications for evolutionary trends in Mexican *Bursera* (Burseraceae). *American Journal of Botany* 86:1047-1057.
- Becerra, J. 2008. Personal communication on Burseraceae (*Bursera*). 5/20/2008.
- Berry, P. E., A. L. Hipp, K. J. Wurdack, B. Van Ee, and R. Riina. 2005. Molecular phylogenetics of the giant genus *Croton* and tribe Crotoneae (Euphorbiaceae sensu stricto) using its and *trnL-trnF* DNA sequence data. *American Journal of Botany* 92:1520-1534.
- Bremer, B., K. Bremer, M. W. Chase, J. L. Reveal, D. E. Soltis, P. S. Soltis, P. F. Stevens, A. A. Anderberg, M. F. Fay, P. Goldblatt, W. S. Judd, M. Kallersjo, J. Karedh, K. A. Kron, J. Lundberg, D. L. Nickrent, R. G. Olmstead, B. Oxelman, J. C. Pires, J. E. Rodman, P. J. Rudall, V. Savolainen, K. J. Sytsma, M. van der Bank, K. Wurdack, J. Q. Y. Xiang, and S. Zmarzty. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141:399-436.
- Bruneau, A., F. Forest, P. S. Herendeen, B. B. Klitgaard, and G. P. Lewis. 2001. Phylogenetic relationships in the Caesalpinoideae (Leguminosae) as inferred from chloroplast *trnL* intron sequences. *Systematic Botany* 26:487-514.
- Chase, M. W., C. M. Morton, and J. A. Kallunki. 1999. Phylogenetic relationships of Rutaceae: A cladistic analysis of the subfamilies using evidence from *rbcL* and *atpB* sequence variation. *American Journal of Botany* 86:1191-1199.
- Chase, M. W., S. Zmarzty, M. D. Lledo, K. J. Wurdack, S. M. Swensen, and M. F. Fay. 2002. When in doubt, put it in Flacourtiaceae: A molecular phylogenetic analysis based on plastid *rbcL* DNA sequences. *Kew Bulletin* 57:141-181.
- Clarkson, J. J., M. W. Chase, and M. M. Harley. 2002. Phylogenetic relationships in Burseraceae based on plastid *rps16* intron sequences. *Kew Bulletin* 57:183-193.

- Corazza-Nunes, M. J., V. M. Novelli, A. L. Olivo Rosas Moreira, W. M. De Carvalho Nunes, S. A. De Carvalho, and M. A. Machado. 2006. The phylogeny of Rutaceae: Contributions from molecular systematics.
- Cornejo, X. 2008. Personal communication on Capparaceae. 6/11/2008.
- Datwyler, S. L. and G. D. Weiblen. 2004. On the origin of the fig: Phylogenetic relationships of moraceae from ndhF sequences. American Journal of Botany 91:767-777.
- Davis, C. C., W. R. Anderson, and M. J. Donoghue. 2001. Phylogeny of Malpighiaceae: Evidence from chloroplast NDHF and TRNL-F nucleotide sequences. American Journal of Botany 88:1830-1846.
- Douglas, N. A. and P. S. Manos. 2007. Molecular phylogeny of Nyctaginaceae: Taxonomy, biogeography, and characters associated with a radiation of xerophytic genera in North America. American Journal of Botany 94:856-872.
- Gottschling, M., J. S. Miller, M. Weigend, and H. H. Hilger. 2005. Congruence of a phylogeny of Cordiaceae (Boraginales) inferred from ITS1 sequence data with morphology, ecology, and biogeography. Annals of the Missouri Botanical Garden 92:425-437.
- Gottschling, M. 2008. Personal communication on Boraginaceae (Cordia). 11/12/2008.
- Grose, S. O. and R. G. Olmstead. 2007. Evolution of a charismatic neotropical clade: Molecular Phylogeny of Tabebuia s. l., crescentiae, and allied genera (Bignoniaceae). Systematic Botany 32:650-659.
- Hall, J. C. 2008. Systematics of Capparaceae and Cleomaceae: An evaluation of the generic delimitations of Capparis and Cleome using plastid DNA sequence data. Botany-Botanique 86:682-696.
- Hall, J. C., K. J. Sytsma, and H. H. Iltis. 2002. Phylogeny of Capparaceae and Brassicaceae based on chloroplast sequence data. American Journal of Botany 89:1826-1842.
- Harrington, M. G., K. J. Edwards, S. A. Johnson, M. W. Chase, and P. A. Gadek. 2005. Phylogenetic inference in Sapindaceae sensu lato using plastid matK and rbcL DNA sequences. Systematic Botany 30:366-382.
- Hu, J. M., M. Lavin, M. F. Wojciechowski, and M. J. Sanderson. 2002. Phylogenetic analysis of nuclear ribosomal ITS/5.8S sequences in the Tribe Millettiae (Fabaceae): Poecilanthe-Cyclolobium, the core Millettiae, and the Callerya group. Systematic Botany 27:722-733.
- Inocencio, C., D. Rivera, M. C. Obon, F. Alcaraz, and J. A. Barrena. 2006. A systematic revision of Capparis section Capparis (Capparaceae). Annals of the Missouri Botanical Garden 93:122-149.
- Kajita, T., H. Ohashi, Y. Tateishi, C. D. Bailey, and J. J. Doyle. 2001. rbcL and legume phylogeny, with particular reference to Phaseoleae, Millettiae, and allies. Systematic Botany 26:515-536.
- Kantz, K. E. and S. C. Tucker. 1997. A phylogenetic analysis of the Caesalpinieae (Leguminosae) using floral developmental and traditional morphological characters. American Journal of Botany 84:206.
- Lavin, M., M. F. Wojciechowski, P. Gasson, C. Hughes, and E. Wheeler. 2003. Phylogeny of robinioid legumes (Fabaceae) revisited: Coursetia and Gliricidia recircumscribed, and a biogeographical appraisal of the Caribbean endemics. Systematic Botany 28:387-409.
- Lavin, M. 2008. Personal communication on Fabaceae (Machaerium, Coursetia). 7/2/2008.
- Lewis, G. 2008. Personal communication on Fabaceae (Acacia, Caesalpinia). 5/21/2008.
- Mabberley, D. J. 2008. Mabberley's plant-book: a portable dictionary of plants, their classification and uses. Third edition. Cambridge University Press, New York.

- Miller, J. S. and J. W. Nowicke. 1989. Sectional placement of some problematic *Cordia* species (Boraginaceae). *Systematic Botany* 14:271-280.
- Miller, J.T. 2008. Personal communication on Fabaceae (Acacia). 6/11/2008.
- Muellner, A. N., R. Samuel, M. W. Chase, A. Coleman, and T. F. Stuessy. 2008. An evaluation of tribes and generic relationships in Melioideae (Meliaceae) based on nuclear ITS ribosomal DNA. *Taxon* 57:98-108.
- Muellner, A. N., R. Samuel, S. A. Johnson, M. Cheek, T. D. Pennington, and M. W. Chase. 2003. Molecular phylogenetics of Meliaceae (Sapindales) based on nuclear and plastid DNA sequences. *American Journal of Botany* 90:471-480.
- Pennington, R. T., M. Lavin, H. Ireland, B. Klitgaard, J. Preston, and J. M. Hu. 2001. Phylogenetic relationships of basal papilionoid legumes based upon sequences of the chloroplast *trnL* intron. *Systematic Botany* 26:537-556.
- Ribeiro, R. A., M. Lavin, J. P. Lemos, C. V. Mendonca, F. R. Dos Santos, and M. B. Lovato. 2007. The genus *Machaerium* (Leguminosae) is more closely related to *Aeschynomene* sect. *Ochopodium* than to *Dalbergia*: Inferences from combined sequence data. *Systematic Botany* 32:762-771.
- Richardson, J. E., M. F. Fay, Q. C. B. Cronk, D. Bowman, and M. W. Chase. 2000. A phylogenetic analysis of Rhamnaceae using *rbcL* and *trnL*-F plastid DNA sequences. *American Journal of Botany* 87:1309-1324.
- Simoes, A. O., T. Livshultz, E. Conti, and M. E. Endress. 2007. Phylogeny and systematics of the Rauvolfioideae (Apocynaceae) based on molecular and morphological evidence. *Annals of the Missouri Botanical Garden* 94:268-297.
- Soltis, D. E., P. S. Soltis, M. W. Chase, M. E. Mort, D. C. Albach, M. Zanis, V. Savolainen, W. H. Hahn, S. B. Hoot, M. F. Fay, M. Axtell, S. M. Swensen, L. M. Prince, W. J. Kress, K. C. Nixon, and J. S. Farris. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society* 133:381-461.
- Stevens, P. F. 2008. Angiosperm Phylogeny Website. Version 9.. Missouri Botanical Garden, Saint Louis, MO.
- Sytsma, K. J., J. Morawetz, J. C. Pires, M. Nepokroeff, E. Conti, M. Zjhra, J. C. Hall, and M. W. Chase. 2002. Urticalean rosids: Circumscription, rosid ancestry, and phylogenetics based on *rbcL*, *trnL*-F, and *ndhF* sequences. *American Journal of Botany* 89:1531-1546.
- Terrazas, T. and M. W. Chase. 1996. A phylogenetic analysis of Anacardiaceae based on morphology, anatomy and *rbcL* sequence data. *American Journal of Botany* 83:197-198.
- Tian, X., Z. H. Guo, and D. Z. Li. 2002. Phylogeny of Aceraceae based on ITS and *trnL*-F data sets. *Acta Botanica Sinica* 44:714-724.
- van Ee, B. 2008. Personal communication on Euphorbiaceae (Croton). 6/10/2008.
- Weiblen, G. D. 2000. Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. *American Journal of Botany* 87:1342-1357.
- Wojciechowski, M. F., M. Lavin, and M. J. Sanderson. 2004. A phylogeny of legumes (Legumenosae) based on analyses of the plastid *matK* gene resolves many well-supported subclades within the family. *American Journal of Botany* 91:1846-1862.
- Wurdack, K. J., P. Hoffmann, and M. W. Chase. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid *rbcL* and *trnL*-F DNA sequences. *American Journal of Botany* 92:1397-1420.
- Zavada, M. S. and M. Kim. 1996. Phylogenetic analysis of Ulmaceae. *Plant Systematics and Evolution* 200:13-20

**Appendix F. Assessing the relationship between NRI and NTI using generalized linear models (GLMs).**

Table 1. The effect of S/G and the CV of S/G on the relationship between NRI and NTI. The sums of squares are calculated first sequentially, with the variance partitioned among the variables according to order of entry; corresponding individual sums of squares are then determined for each variable only after *all* other variables have been entered. The table shows that once S/G is entered into the model, NTI is able to account for a significant proportion of the remaining variation in NRI for both the full and non-Fabaceae trees; in all three trees, where the addition of S/G does not have a significant impact on the NRI/NTI relationship, there is still an increase in the proportion of remaining variation in NRI for which NTI is able to account (shown as increase between sequential and adjusted sum of squares for NTI).

NRI versus:																
Full							Fabaceae							Non-Fabaceae		
Source	DF	Seq SS	Adj SS	Adj MS	F	p	Seq SS	Adj SS	Adj MS	F	P	Seq SS	Adj SS	Adj MS	F	P
NTI	1	2.381	10.813	10.813	14.48	<0.001	0.1178	1.9208	1.9208	2.54	0.119	1.5971	3.4389	3.4389	6.31	0.016
S/G	1	34.509	34.509	34.509	46.21	<0.001	7.8932	7.8932	7.8932	10.43	0.002	11.0663	11.0663	11.0663	20.31	<0.001
Error	40	29.873	29.873	0.747			30.2708	30.2708	0.7568			21.7943	21.7943	0.5449		
Total	42	66.763					38.2818					34.4577				
R <sup>2</sup>		55.26%					20.93%					36.75%				
NTI	1	2.381	4.293	4.293	4.12	0.049	0.1178	0.5397	0.5397	0.65	0.423	1.5971	1.5882	1.5882	2.49	0.122
CV of S/G	1	22.692	22.692	22.692	21.77	0.016	5.171	5.171	5.171	6.27	0.016	7.3822	7.3822	7.3822	11.59	0.002
Error	40	41.69	41.69	1.042			32.993	32.993	0.8248			25.4784	25.4784	0.6370		
Total	42	66.763					38.2818					34.4577				
R <sup>2</sup>		37.55%					13.82%					26.06%				
NTI	1	2.381	10.856	10.856	14.30	0.001	0.1178	2.1063	2.1063	2.73	0.106	1.5971	3.2971	3.2971	5.9	0.02
S/G	1	34.509	34.509	34.509	15.91	<0.001	7.8932	2.9227	2.9227	3.79	0.059	11.0663	11.0663	11.0663	6.62	0.014
CV of S/G	1	0.261	0.261	0.261	0.34	0.561	0.2005	0.2005	0.2005	0.26	0.613	0.0131	0.0131	0.0131	0.02	0.879
Error	39	29.612	29.612	0.759			30.0703	30.0703	0.771			21.7811	21.7811	0.5585		
Total	42	66.763					38.2818					34.4577				
R <sup>2</sup>		55.65%					21.45%					39.79%				