Growth strategies in the saplings of tree species differing in adult sizes in a Central Amazon forest

Marcel Vaz

Abstract

The coexistence of several hundreds of tree species in tropical forests is a long standing challenge for ecologists. Specially intriguing is the coexistence of tree species with different adult sizes. It has been suggested that canopy trees, when young, tend to grow quickly upwards, thus reaching higher light levels before their competitors, what would help to explain their dominance over the shorter understory species. If that is the case, then these taller species must be able to maximize their growth in height (height gain efficiency, HGE), which should be reflected in their height-mass ratio. I here tested this prediction by modeling the HGE of 325 saplings from 89 different species as a linear function of their size as adults. In my analysis I allowed trees' responses to vary according to their species by inserting parameters such as μ_i and τ_i (mean and precision). The parameters of interest was the regression intercept (β_0) and, specially, slope (β_1). Priors for these parameters were determined using extreme values found in my own dataset. Results, contrary to prediction, showed that taller trees are actually less efficient at growing taller than understory trees, at least when both are in the understory. This may indicate that saplings from taller do not have a competitive advantage agains the saplings of shorter species, and this may be the reason why canopy species never happen to exclude the species that live under their domain.

Introduction

Tropical forests has always amazed people due to the fascinating biological diversity they harbor. What really intrigues biologists, though, is not diversity per se, but the eco-evolutionary processes and mechanisms that allow for such diversity to be created and maintained. The solution to this nature's riddle sounds even more difficult when it comes to plants, that have to fight for exactly the same resources (mostly sun light and soil nutrients). After all, how could so many competitor species coexist without excluding each other?

Although plants share their basic requirements needed to survive, grow, and reproduce, the ways they accomplish these basic tasks are highly variable. Such strategies can be divided between acquisition and use strategies. Plants can be very aggressive investors in acquisition of resources by investing most of their photosynthetic gains into producing more "absorptive" organs, like leaves

and fine roots, depending on what resource is the one that most limits their growth. Plants also can be very competitive just by maximizing the returns of their investments, and thus decreasing the minimum resource needed to survive, as by having low metabolic rates, e.g.

Coexistence, which can be defined as the ad aeternum co-occurence of two or more species in a given, arbitrarily delimited area, follows what is known as the R* rule of competition:

$$R^* = \frac{d}{a * e} \tag{1}$$

where R^* is the resource level when population size is at equilibrium, d is the mortality rate, a is the resource uptake/acquisition efficiency, and e is the resource use efficiency. According to this rule, the stronger competitor species in a given area will be the one that has the lowest R^*. Equation 1 shows that a very competitive species could be made with low d and high a and e values. In nature, however, the existence of this super-competitor is very unlikely given that a set of constraints, such as the exponentially increasing maintenance costs of body size, may limit the benefits of investing in resource acquisition, e.g. On the same token, it can be observed that species with different a and e values can have similar competitive ability provided d and the product $a * e$ are held constant. In other words, a trade-off between resource acquisition efficiency and resource use efficiency could facilitate coexistence of competitor species.

This theoretical background seems to be supported by two earlier classifications of tropical forest tree species: pioneer vs. late-successional and canopy and understory species. Pioneer species have high d in the understory, and thus will not be considered here. Late-successional species, on the other hand, tend to tolerate well low light levels, and are believed differentiate along the previously mentioned trade-off: canopy trees are efficient at intercepting light, whereas understory trees excel at using low light levels to grow. Central to this hypothesis, is the ability of saplings canopy species to grow in height faster than the other species in the understory. The realization of such fast growth, however, could only be possible if the plant do not invest in lateral branches, which in turn would increase light interception in the understory. Investment in a wider crown imposes a heavier load on the stem, which would need to be thicker and heavier. It is clear, therefore, that there is a mechanical trade-off between crown width and height gain efficiency (HGE). While crown width maximizes light harvest in the shady conditions of the understory,

height gain allows canopy species to intercept light preemptively and to reach the canopy faster.

In this paper I tested whether canopy trees tend to have higher HGE values as saplings than other understory species. In my analysis I used height:mass ratios (a proxy for HGE) measured for 325 saplings from 89 different species found in the understory of a hyper-diverse forest in Central Amazon. The sampled species make up a small fraction of an estimated pool of more than 1,000 tree species, most of which occur at very low densities (<1 tree per hectare), and have adult sizes that range from 5 to 40 m tall.

Methods

Height gain efficiency was measured as the ratio between crown height (m) and estimated plant dry mass (kg). Plant dry mass was estimated as the product of volume (cm^3) and the density ($kg.cm^{-3}$) of the stem. Stem volume was estimated as the volume of a cone, where the stem base diameter was measured at 10 cm above the ground and the height of the main stem was used as the cone's height. Stem density was estimated as the ratio between dry weight (kg) and fresh volume (cm^3) a twig section. Adult size (m) was estimated as the 97.5% quantile of the diameter at breat height (later converted into height with an allometric equation specifically developed for the studied forest) of all trees found in a contiguous 25 hectare plot. In this plot, all plants starting at 1 cm DBH were tagged, mapped and identified. I later used data from other 20 1-hectare plots (DBH starting at 10 cm) spread over the region to update these 97.5% quantiles and increase the confidence on adult size for most species. In order to analyze these data (shown in Fig.1 and Tab.1), I used a random effects model, allowing the mean and variance of the response variable to vary between species.

For i ranging from 1 to S, the number of species in the sample ($S = 89$), and j ranging from 1 to I, the number of individuals of each species in the sample ($1 \leq I \leq 9$) the model follows:

$$y_{ij} \sim No(\mu_i, \tau_i) \tag{2}$$
$$\mu_i = \beta_0 + \beta_1 * x_i + \beta_i \tag{3}$$
$$\beta_i \sim No(0, \tau_b) \tag{4}$$
$$\tau_i \sim Uniform(a, b) \tag{5}$$
$$\beta_0 \sim No(m_0, \tau_0) \tag{6}$$
$$\beta_1 \sim No(0, \tau) \tag{7}$$

where the observed HGE (y) of the jth tree belonging to the ith species is modeled as a random draw from a normal distribution (Eq.2) with mean μ_i and precision τ_i, both specific for the ith species. μ_i, in turn, was modeled as a linear function of adult size of each species (x_i), with intercept β_0, slope β_1, and a species effect β_i (Eq.3). The species effect (β_i) was modeled as random draw from a normal distribution centered at zero and with precision of τ_b (Eq.4). Species specific precision (τ_i) was modeled as a draw from a uniform distribution restricted between a and b (Eq.5). The intercept of the linear regression was modeled as draw from normal distribution with mean m_0 and precision τ_0 (Eq.6). Last, the slope of the regression was modeled as a draw from a normal centered at zero and with precision τ (Eq.7).

There was a total six constants in the model (τ_b, a, b, m_0, τ_0, and τ). I started by setting the prior for the intercept (β_0), which should be a value of HGE when adult size is zero. Of course this is not the case for trees, but as adult size tends to zero, also does HGE (crown height divided by stem dry mass), so it is safe to assume the intercept should never be negative. Regarding β_0 upper limit, it is reasonable to assume a plant with a stem that weights 2 kg (1 kg when dry) would never surpass a height of 10 m. Therefore, using the range method ($0 < \beta_0 < 10 m.kg^{-1}$), τ_0 could be estimated as 0.16. I also assumed the prior distribution of the intercept would be symmetric, meaning that its mean m_0 should be around 5 $m.kg^{-1}$. Using the same reasoning, I set the precision of β_i to be also 0.16 and the upper limit of the prior distribution of τ_i to be 0.16. The lower limit for τ_i was assumed to be 100, as, in principle, plants from the same species may not vary in HGE. Finally, to determine the prior of the slope, I used the observed ranges of HGE and adult size in order to estimate the range of possible values for β_1. This was done by calculating a slope for two hypothetical plants, one with maximum HGE and adult size, and the other with the minimum of both. This thought "experiment" resulted in a range for the slope between 0.2 and -0.2. Through the range method, I assumed the precision for this prior (τ) was 97.97.

The whole analysis was run in JAGS through R; the code for the model used in JAGS is on page 11, and the script used in R to run the analyses and produce the graphics is on page 11. The model was run for 501000 times.

Results

Temporal auto-correlation between posterior samples vanished after a few time steps (Fig.2) and time series plots (Fig.3) show that MCMC had a rapid convergence (the first 1000 simulations were discarded). Main results are shown in Tables 2-4.

Posterior distributions of β_i show that, despite some variation, species effect was always close to zero; only one species had a significant positive effect on HGE (Fig.4; Tab.2). However, because the slope was very close to zero (Fig.5; Tab.2), the species random effect is what explains most of variation in HGE, as it can be seen by the similarity between the estimates of β_i and μ_i (Fig.4; Tab.3), the difference being in scale and, thus, caused by the intercept, which was significantly greater than zero (Fig.5; Tab.2). Finally, the estimated precisions for the species effect were not very different from the piors (Fig.4; Tab.4). This is probably due to the high number of singletons in the sampling (32 out of the 89 species sampled). For the species that had more replicates, though, it could be seen that precision is usually very low, indicating that HGE is a highly variable trait.

In order to evaluate the degree to which the choice of priors affected the results, I performed a sensitivity analysis (31000 simulations, excluding the first 1000 ones) by wiggling four of the six constants used to define the prior distributions: the mean of β_0, the minimum limit of τ_i and the precisions of β_1 and β_i. Results showed that the only constants that could change the posterior distribution of the slope are m_0 and τ_b. Although increasing τ_b could potentially lead to a significant result, this is hardly the case, as the posterior distribution for β_1 is well centered at zero (Fig.6). More problematic, though, is the effect of m_0, which has the potential to even switch the sign of the slope (Fig.6).

Conclusion

This analysis showed that here is no evidence of the often assumed relationship between adult size and height gain efficiency, with most of the variation in HGE explained by the differences among species. My sensitivity analysis, though, revealed that the definition of the prior for the intercept has the potential to affect the conclusions above, and for this reason should be done with more caution. I propose to elaborate a better prior, based on empirical evidence to validate these results.

Appendix

Figures
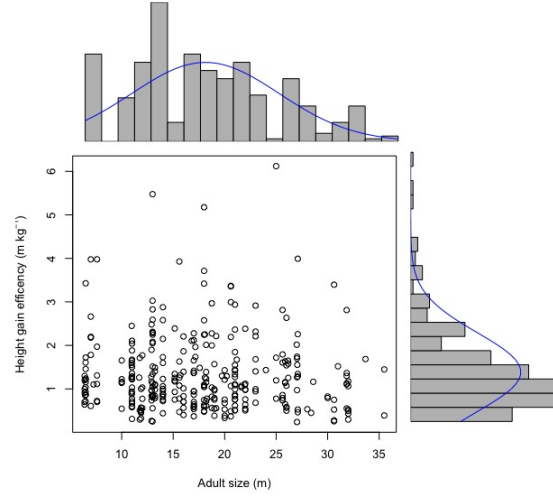
Figure 1: Mean height gain efficiency and adult size of 325 young trees from 89 species.
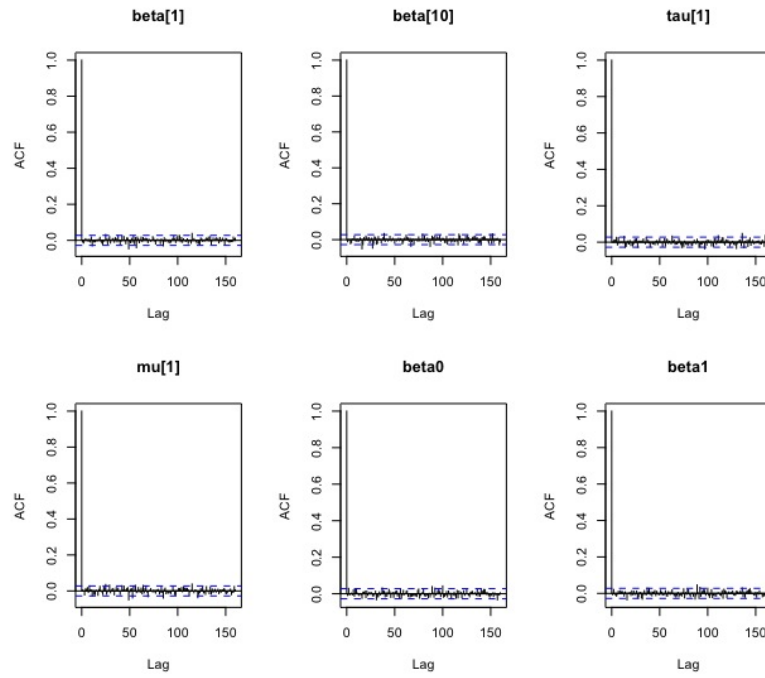
Figure 2: Sample of autocorrelation plots for some parameters.
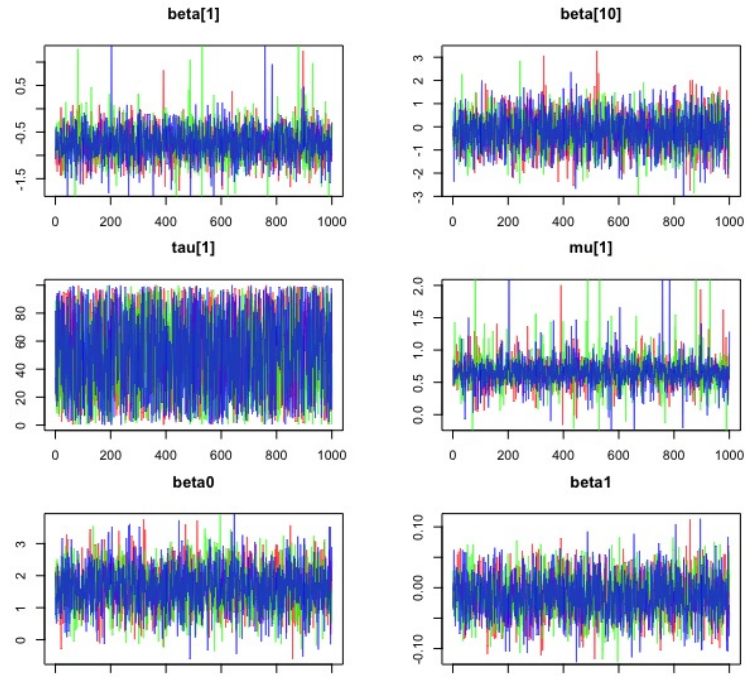
Figure 3: Sample of time-series plots for some parameters.

Figure 4: Posterior distributions of the species-specific parameters (β_i, μ_i, and τ_i).

Figure 5: Prior and posterior distributions of β_0 and β_1.

Figure 6: Effect of changing four constants (τ, m_0, τ_b, and a) on the regression slope, β_1.

Tables

Table 1: Sample size (n), mean height gain efficiency (HGE; $m.kg^{-1}$), and adult size (m) for each of the sampled species.

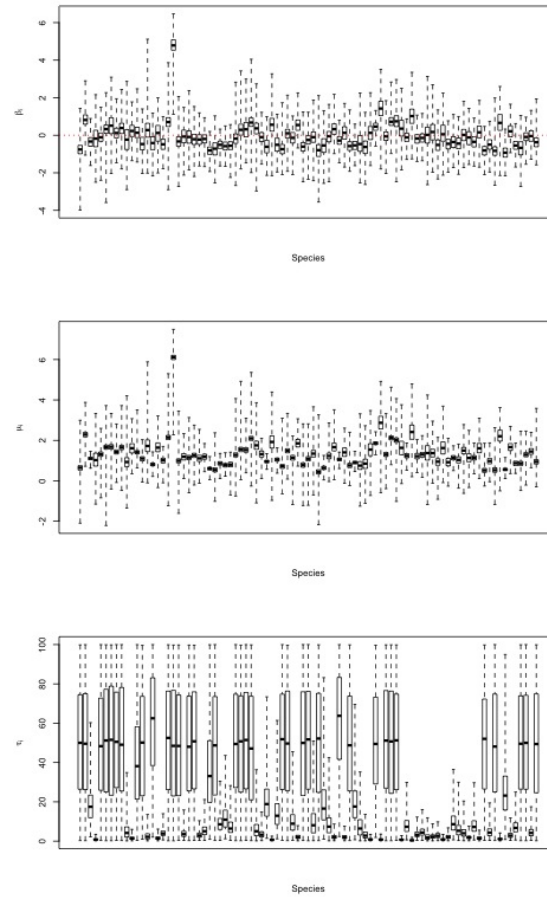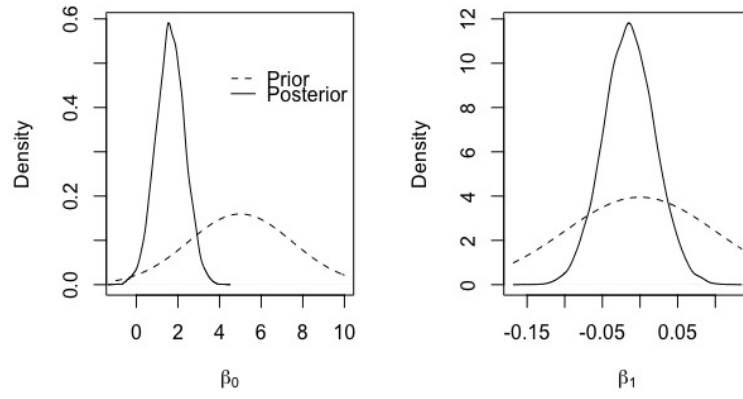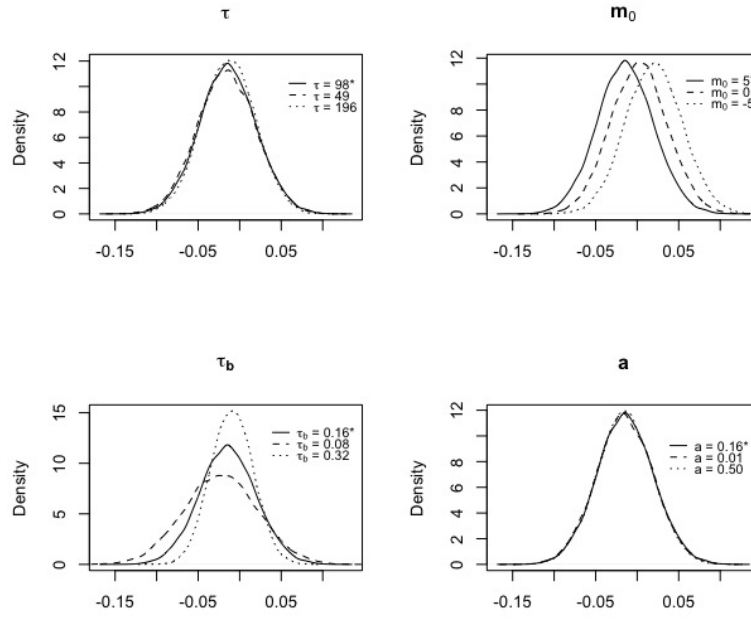| Code	Species	HGE	Size	n	Code	Species	HGE	Size	n
1	Amaioua corymbosa	0.64	17.02	1.00	46	Mabea speciosa	1.35	14.00	2.00
2	Amaioua guianensis	2.30	13.00	1.00	47	Manilkara cavalcantei	0.45	28.40	1.00
3	Amphirrhox longifolia	1.10	13.22	7.00	48	Manilkara huberi	0.63	32.00	4.00
4	Anacardium parvifolium	1.04	30.62	5.00	49	Mezilaurus duckei	1.23	25.00	3.00
5	Aniba riparia	1.32	15.70	1.00	50	Micrandropsis scleroxylon	1.70	21.00	6.00
6	Anisophyllea manausensis	1.67	21.18	1.00	51	Micropholis guyanensis	1.06	21.62	2.00
7	Aspidosperma carapanauba	1.69	33.67	1.00	52	Minquartia guianensis	1.43	25.62	6.00
8	Astronium lecointei	1.43	24.00	1.00	53	Myrcia grandis	0.76	22.00	1.00
9	Brosimum rubescens	1.65	26.15	1.00	54	Naucleopsis caloneura	0.90	14.00	6.00
10	Buchenavia grandis	0.92	35.50	2.00	55	Ocotea canaliculata	0.74	32.00	2.00
11	Casearia javitensis	1.61	18.75	6.00	56	Ouratea coccinea	0.84	11.76	3.00
12	Chrysophyllum lucentifolium	1.42	26.18	2.00	57	Ouratea discophora	1.52	15.60	6.00
13	Compsoneura ulei	1.10	7.26	1.00	58	Paramachaerium ormosoides	1.85	17.16	2.00
14	Coussarea ampla	1.72	12.90	2.00	59	Pausandra macropetala	2.96	13.00	6.00
15	Duckeodendron cestroides	0.81	30.00	2.00	60	Pourouma tomentosa	1.29	20.20	1.00
16	Duguetia asterotricha	1.65	6.50	6.00	61	Pouteria campanulata	2.12	17.00	1.00
17	Duguetia flagellaris	1.00	11.00	9.00	62	Pouteria hispida	2.02	27.00	1.00
18	Duroia macrophylla	2.15	14.00	1.00	63	Pouteria resinosa	1.65	27.10	6.00
19	Ecclinusa guianensis	6.12	25.00	1.00	64	Pouteria reticulata	1.23	21.00	6.00
20	Eperua glabriflora	1.00	23.00	1.00	65	Protium decandrum	2.47	18.00	7.00
21	Erisma bicolor	1.18	27.02	5.00	66	Protium hebetatum	1.21	17.00	7.00
22	Erisma fuscum	1.16	28.60	1.00	67	Protium opacum	1.29	15.15	7.00
23	Erythroxylum macrophyllum	1.26	11.70	1.00	68	Protium paniculatum	1.39	19.18	2.00
24	Eschweilera coriacea	1.11	22.00	6.00	69	Protium pilosissimum	1.38	31.85	6.00
25	Eschweilera grandiflora	1.19	18.20	6.00	70	Protium trifoliolatum	0.93	13.00	6.00
26	Eschweilera pedicellata	0.60	16.00	3.00	71	Rinorea amapensis	1.63	7.60	6.00
27	Eschweilera pseudodecolorans	0.53	28.02	1.00	72	Rinorea guianensis	0.92	18.00	7.00
28	Eschweilera romeu-cardosoi	0.86	19.00	7.00	73	Rinorea macrocarpa	1.14	10.00	5.00
29	Eschweilera truncata	0.78	21.00	6.00	74	Rinorea racemosa	1.03	12.00	4.00
30	Eschweilera wachenheimii	0.80	20.00	6.00	75	Ryania speciosa	1.50	10.97	5.00
31	Eugenia cupulata	1.28	12.88	1.00	76	Scleronema micranthum	1.15	26.00	6.00
32	Geissospermum argenteum	1.55	27.05	1.00	77	Siparuna cuspidata	1.14	10.97	6.00
33	Goupia glabra	1.52	31.00	1.00	78	Siparuna decipiens	1.59	14.00	6.00
34	Guarea carinata	2.11	16.80	1.00	79	Sloanea floribunda	0.51	22.00	1.00
35	Guatteria olivacea	1.76	18.07	2.00	80	Sorocea muriculata	0.98	12.90	6.00
36	Gustavia elliptica	1.31	16.00	6.00	81	Symphonia globulifera	0.53	20.00	1.00
37	Henriettella caudata	0.96	6.40	6.00	82	Tabernaemontana muricata	2.23	7.00	6.00
38	Hevea guianensis	1.98	20.60	7.00	83	Tapura guianensis	0.56	11.88	6.00
39	Hirtella myrmecophila	1.05	6.49	6.00	84	Theobroma sylvestre	1.66	13.00	6.00
40	Inga umbratica	0.72	14.00	1.00	85	Unonopsis duckei	0.86	17.00	6.00
41	Lecythis barnebyi	1.48	17.57	1.00	86	Vismia sandwithii	0.85	6.45	1.00
42	Lecythis prancei	1.14	25.88	4.00	87	Zollernia paraensis	1.30	19.73	1.00
43	Licania heteromorpha	1.87	23.00	6.00	88	Zygia juruana	1.45	11.00	6.00
44	Licania octandra	0.78	18.27	1.00	89	Zygia racemosa	0.95	23.00	1.00
45	Licaria cannella	1.09	21.95	1.00	45				

Table 2: Descriptive statistics of the posterior samples taken for all estimated betas.

	mu.vect	sd.vect	2.5%	97.5%		mu.vect	sd.vect	2.5%	97.5%
beta0	1.636	0.694	0.265	2.981	beta[45]	-0.231	0.367	-0.92	0.462
beta1	-0.014	0.034	-0.081	0.054	beta[46]	-0.094	0.459	-1.003	0.816
beta[1]	-0.744	0.355	-1.412	-0.063	beta[47]	-0.774	0.482	-1.705	0.172
beta[2]	0.84	0.407	0.061	1.626	beta[48]	-0.55	0.543	-1.615	0.506
beta[3]	-0.348	0.339	-1.011	0.311	beta[49]	-0.05	0.427	-0.895	0.788
beta[4]	-0.153	0.711	-1.558	1.262	beta[50]	0.354	0.41	-0.457	1.165
beta[5]	-0.096	0.368	-0.791	0.604	beta[51]	-0.271	0.308	-0.864	0.34
beta[6]	0.337	0.364	-0.339	1.02	beta[52]	0.155	0.478	-0.779	1.101
beta[7]	0.523	0.621	-0.715	1.728	beta[53]	-0.555	0.367	-1.24	0.157
beta[8]	0.135	0.4	-0.625	0.902	beta[54]	-0.533	0.328	-1.162	0.117
beta[9]	0.381	0.433	-0.467	1.209	beta[55]	-0.434	0.645	-1.687	0.847
beta[10]	-0.203	0.753	-1.658	1.281	beta[56]	-0.617	0.536	-1.675	0.432
beta[11]	0.235	0.456	-0.678	1.134	beta[57]	0.103	0.558	-1.003	1.2
beta[12]	0.152	0.401	-0.638	0.942	beta[58]	0.457	0.303	-0.135	1.041
beta[13]	-0.425	0.525	-1.447	0.59	beta[59]	1.444	0.585	0.254	2.578
beta[14]	0.255	0.659	-1.119	1.575	beta[60]	-0.053	0.361	-0.727	0.626
beta[15]	-0.402	0.483	-1.36	0.547	beta[61]	0.723	0.359	0.054	1.406
beta[16]	0.109	0.604	-1.075	1.29	beta[62]	0.759	0.457	-0.113	1.645
beta[17]	-0.473	0.413	-1.301	0.34	beta[63]	0.385	0.631	-0.847	1.635
beta[18]	0.708	0.386	-0.022	1.436	beta[64]	-0.108	0.321	-0.72	0.535
beta[19]	4.79	0.452	3.923	5.592	beta[65]	1.023	0.634	-0.255	2.239
beta[20]	-0.31	0.383	-1.039	0.431	beta[66]	-0.183	0.351	-0.868	0.512
beta[21]	-0.066	0.468	-0.994	0.853	beta[67]	-0.13	0.351	-0.813	0.568
beta[22]	-0.067	0.488	-1.016	0.89	beta[68]	0.023	0.674	-1.337	1.38
beta[23]	-0.206	0.419	-1.017	0.6	beta[69]	0.191	0.605	-0.997	1.383
beta[24]	-0.215	0.391	-0.984	0.545	beta[70]	-0.525	0.427	-1.372	0.321
beta[25]	-0.189	0.335	-0.846	0.456	beta[71]	0.103	0.652	-1.186	1.385
beta[26]	-0.807	0.306	-1.403	-0.196	beta[72]	-0.45	0.385	-1.2	0.306
beta[27]	-0.699	0.477	-1.625	0.217	beta[73]	-0.347	0.435	-1.205	0.502
beta[28]	-0.508	0.302	-1.095	0.088	beta[74]	-0.422	0.433	-1.268	0.429
beta[29]	-0.562	0.308	-1.161	0.054	beta[75]	0.018	0.45	-0.876	0.901
beta[30]	-0.548	0.323	-1.174	0.099	beta[76]	-0.113	0.49	-1.084	0.852
beta[31]	-0.174	0.403	-0.952	0.604	beta[77]	-0.342	0.411	-1.147	0.479
beta[32]	0.302	0.457	-0.584	1.184	beta[78]	0.153	0.48	-0.8	1.086
beta[33]	0.326	0.546	-0.733	1.39	beta[79]	-0.808	0.37	-1.503	-0.087
beta[34]	0.707	0.358	0.02	1.391	beta[80]	-0.47	0.397	-1.246	0.302
beta[35]	0.367	0.49	-0.582	1.331	beta[81]	-0.812	0.362	-1.479	-0.138
beta[36]	-0.09	0.373	-0.814	0.649	beta[82]	0.679	0.636	-0.574	1.933
beta[37]	-0.586	0.508	-1.581	0.415	beta[83]	-0.91	0.365	-1.626	-0.185
beta[38]	0.606	0.549	-0.506	1.677	beta[84]	0.204	0.427	-0.628	1.042
beta[39]	-0.491	0.51	-1.476	0.524	beta[85]	-0.525	0.323	-1.148	0.107
beta[40]	-0.714	0.386	-1.448	0.024	beta[86]	-0.685	0.548	-1.752	0.393
beta[41]	0.099	0.353	-0.557	0.775	beta[87]	-0.057	0.35	-0.718	0.611
beta[42]	-0.124	0.409	-0.933	0.671	beta[88]	-0.026	0.432	-0.876	0.816
beta[43]	0.554	0.433	-0.3	1.406	beta[89]	-0.358	0.38	-1.087	0.374
beta[44]	-0.597	0.351	-1.252	0.083					

Table 3: Descriptive statistics of the posterior samples taken for all estimated mus.

	mu.vect	sd.vect	2.5%	97.5%		mu.vect	sd.vect	2.5%	97.5%
mu[1]	0.65	0.228	0.236	1.059	mu[46]	1.343	0.34	0.658	2.01
mu[2]	2.292	0.24	1.849	2.71	mu[47]	0.458	0.235	0.039	0.886
mu[3]	1.1	0.1	0.899	1.3	mu[48]	0.63	0.144	0.34	0.91
mu[4]	1.047	0.544	-0.048	2.169	mu[49]	1.23	0.257	0.704	1.746
mu[5]	1.317	0.233	0.889	1.737	mu[50]	1.691	0.311	1.069	2.321
mu[6]	1.672	0.237	1.252	2.084	mu[51]	1.058	0.122	0.832	1.29
mu[7]	1.68	0.233	1.224	2.111	mu[52]	1.427	0.326	0.768	2.088
mu[8]	1.43	0.235	1.005	1.855	mu[53]	0.768	0.232	0.345	1.205
mu[9]	1.645	0.23	1.225	2.078	mu[54]	0.904	0.109	0.692	1.125
mu[10]	0.927	0.435	0.047	1.786	mu[55]	0.747	0.384	-0.022	1.537
mu[11]	1.604	0.377	0.842	2.336	mu[56]	0.852	0.41	0.023	1.693
mu[12]	1.415	0.167	1.101	1.735	mu[57]	1.517	0.487	0.548	2.498
mu[13]	1.108	0.238	0.678	1.542	mu[58]	1.849	0.14	1.581	2.111
mu[14]	1.708	0.58	0.501	2.885	mu[59]	2.895	0.495	1.87	3.86
mu[15]	0.807	0.116	0.59	1.028	mu[60]	1.296	0.239	0.881	1.711
mu[16]	1.653	0.365	0.911	2.383	mu[61]	2.118	0.236	1.693	2.554
mu[17]	1.007	0.18	0.653	1.363	mu[62]	2.01	0.241	1.563	2.436
mu[18]	2.145	0.237	1.709	2.554	mu[63]	1.635	0.506	0.635	2.638
mu[19]	6.07	0.3	5.486	6.474	mu[64]	1.229	0.167	0.895	1.566
mu[20]	0.999	0.238	0.561	1.438	mu[65]	2.403	0.582	1.215	3.545
mu[21]	1.185	0.271	0.655	1.73	mu[66]	1.211	0.226	0.755	1.666
mu[22]	1.162	0.234	0.735	1.608	mu[67]	1.291	0.197	0.897	1.684
mu[23]	1.264	0.231	0.839	1.696	mu[68]	1.386	0.628	0.057	2.657
mu[24]	1.108	0.267	0.574	1.647	mu[69]	1.374	0.31	0.757	2.003
mu[25]	1.188	0.207	0.767	1.599	mu[70]	0.926	0.278	0.372	1.488
mu[26]	0.602	0.124	0.355	0.853	mu[71]	1.631	0.478	0.683	2.571
mu[27]	0.538	0.237	0.123	0.962	mu[72]	0.93	0.282	0.369	1.507
mu[28]	0.858	0.144	0.568	1.145	mu[73]	1.147	0.173	0.806	1.499
mu[29]	0.776	0.138	0.508	1.047	mu[74]	1.044	0.26	0.535	1.561
mu[30]	0.804	0.18	0.454	1.162	mu[75]	1.498	0.259	0.98	2.02
mu[31]	1.279	0.234	0.855	1.71	mu[76]	1.153	0.335	0.477	1.826
mu[32]	1.554	0.246	1.109	1.974	mu[77]	1.138	0.17	0.799	1.479
mu[33]	1.521	0.226	1.102	1.948	mu[78]	1.59	0.373	0.847	2.332
mu[34]	2.104	0.231	1.685	2.518	mu[79]	0.515	0.233	0.113	0.96
mu[35]	1.746	0.417	0.9	2.586	mu[80]	0.982	0.219	0.543	1.41
mu[36]	1.318	0.25	0.826	1.831	mu[81]	0.539	0.248	0.112	0.981
mu[37]	0.96	0.109	0.739	1.178	mu[82]	2.216	0.434	1.336	3.085
mu[38]	1.949	0.476	0.966	2.885	mu[83]	0.557	0.095	0.365	0.748
mu[39]	1.053	0.127	0.796	1.305	mu[84]	1.655	0.276	1.106	2.211
mu[40]	0.723	0.235	0.295	1.164	mu[85]	0.869	0.175	0.522	1.22
mu[41]	1.485	0.233	1.048	1.922	mu[86]	0.86	0.234	0.419	1.299
mu[42]	1.144	0.201	0.745	1.544	mu[87]	1.298	0.23	0.882	1.71
mu[43]	1.862	0.314	1.228	2.493	mu[88]	1.454	0.221	1.011	1.9
mu[44]	0.78	0.232	0.366	1.212	mu[89]	0.95	0.231	0.534	1.395
mu[45]	1.092	0.232	0.66	1.509					

Table 4: Descriptive statistics of the posterior samples taken for all estimated taus.

	mu.vect	sd.vect	2.5%	97.5%		mu.vect	sd.vect	2.5%	97.5%
tau[1]	50.17	28.82	2.977	97.624	tau[46]	10.136	8.244	0.793	31.996
tau[2]	50.518	28.804	2.88	97.697	tau[47]	50.587	28.936	2.889	97.495
tau[3]	18.941	9.461	5.244	41.096	tau[48]	19.635	12.433	3.248	49.651
tau[4]	0.867	0.479	0.223	2.051	tau[49]	9.032	6.364	1.158	25.043
tau[5]	49.889	28.679	2.811	97.421	tau[50]	2.34	1.26	0.559	5.397
tau[6]	50.628	28.89	2.962	97.915	tau[51]	59.937	26.093	9.119	98.24
tau[7]	49.904	28.859	2.691	97.45	tau[52]	2.132	1.12	0.54	4.778
tau[8]	50.54	28.74	2.799	97.571	tau[53]	50.401	28.874	2.818	97.419
tau[9]	50.311	28.611	2.888	97.453	tau[54]	19.285	10.232	3.414	43.453
tau[10]	5.484	4.433	0.465	17.052	tau[55]	7.845	6.28	0.675	24.18
tau[11]	1.572	0.836	0.406	3.597	tau[56]	3.44	2.416	0.459	9.643
tau[12]	41.329	25.807	3.593	94.269	tau[57]	0.916	0.475	0.25	2.064
tau[13]	49.915	28.835	2.817	97.492	tau[58]	50.555	26.883	5.479	96.966
tau[14]	2.677	2.114	0.297	8.194	tau[59]	0.863	0.452	0.238	1.954
tau[15]	59.864	26.215	8.353	98.214	tau[60]	50.629	28.557	2.917	97.509
tau[16]	1.667	0.88	0.424	3.807	tau[61]	49.747	28.667	2.627	97.127
tau[17]	4.222	1.882	1.387	8.561	tau[62]	49.915	28.736	2.802	97.134
tau[18]	50.378	28.747	2.762	97.544	tau[63]	0.813	0.418	0.232	1.825
tau[19]	49.445	29.161	2.095	97.41	tau[64]	8.154	4.415	1.946	18.972
tau[20]	49.512	28.81	2.7	97.45	tau[65]	0.486	0.225	0.183	1.032
tau[21]	3.939	2.26	0.854	9.49	tau[66]	3.609	1.789	1.001	7.909
tau[22]	49.938	28.942	2.766	97.288	tau[67]	4.859	2.441	1.306	10.686
tau[23]	50.579	28.665	2.944	97.597	tau[68]	2.255	1.755	0.279	6.793
tau[24]	3.173	1.674	0.773	7.192	tau[69]	2.411	1.294	0.586	5.539
tau[25]	5.465	2.956	1.305	12.612	tau[70]	2.971	1.592	0.701	6.793
tau[26]	38.05	23.099	5.145	90.484	tau[71]	0.925	0.484	0.248	2.087
tau[27]	50.115	28.633	2.799	97.42	tau[72]	2.311	1.154	0.644	5.075
tau[28]	9.17	4.574	2.444	20.176	tau[73]	9.568	5.467	2.025	23.042
tau[29]	11.967	6.354	2.88	27.186	tau[74]	5.977	3.794	1.011	15.46
tau[30]	7.18	3.851	1.686	16.445	tau[75]	4.455	2.584	0.929	10.757
tau[31]	50.009	28.62	2.983	97.603	tau[76]	2.038	1.085	0.487	4.687
tau[32]	49.746	28.736	2.685	97.348	tau[77]	8.141	4.335	1.998	18.547
tau[33]	50.263	28.909	2.744	97.635	tau[78]	1.616	0.868	0.397	3.718
tau[34]	49.845	28.685	2.865	97.535	tau[79]	50.371	28.711	2.865	97.628
tau[35]	6.231	4.958	0.529	19.292	tau[80]	4.748	2.5	1.184	10.909
tau[36]	3.587	1.947	0.884	8.254	tau[81]	49.843	28.615	2.767	97.509
tau[37]	20.221	10.882	4.858	46.528	tau[82]	1.164	0.617	0.294	2.655
tau[38]	0.76	0.373	0.235	1.657	tau[83]	25.837	13.689	6.439	58.88
tau[39]	14.511	7.861	3.413	33.784	tau[84]	3.026	1.622	0.734	6.964
tau[40]	50.361	28.595	2.795	97.37	tau[85]	7.521	4.017	1.822	17.169
tau[41]	49.989	28.95	2.688	97.492	tau[86]	50.224	28.536	2.856	97.52
tau[42]	10.326	6.436	1.786	26.367	tau[87]	50.452	28.599	2.934	97.501
tau[43]	2.282	1.216	0.546	5.237	tau[88]	4.606	2.459	1.092	10.476
tau[44]	50.536	28.748	2.989	97.626	tau[89]	50.357	28.67	2.752	97.462
tau[45]	50.707	28.769	2.985	97.522					

JAGS model

```
model{

  # LIKELIHOOD
  for(i in 1:ss){
    for(j in 1:is[i]){
      y[i,j] ~ dnorm(mu[i],tau[i])
    }
    mu[i] = beta0 + x[i]*beta1 + beta[i]
    beta[i] ~ dnorm(0,taub)
    tau[i] ~ dunif(ai,bi)
  }

  # PRIORS
  beta0 ~ dnorm(m0,tau0)
  beta1 ~ dnorm(0,tau1)

}
```

R script

```
#### FINAL DAP R SCRIPT
### PACKAGES
# Loading packages
library(R2jags)
library(lattice)
library(ggplot2)
library(xtable)
source("AddBurnin.R")

### DATA
dd = read.csv("HGEvsAS.csv",header=T,as.is=T) # data set
dd$hge = dd$hge/10 # scale correction
head(dd)
str(dd)

ss = length(unique(dd$sp)) # total number of species
is = table(dd$sp) # sampling size of each species

## Table 0. Data
tab0 = aggregate(cbind(hge,aSize)~sp,dd,mean)
tab0=cbind(tab0,as.numeric(is))
names(tab0) = c("Species","HGE","Size","n")
tab0a = tab0[1:ceiling(nrow(tab0)/2),]
tab0b = rbind(tab0[ceiling(nrow(tab0)/2+1):nrow(tab0),],rep(NA,4))
tab0f = cbind(tab0a,cbind(row.names(tab0b),tab0b))
head(tab0f)
tail(tab0f)
xtable(tab0f)

## Figure 0. Data
require(mvtnorm)
source("scatterBarNorm.R")
scatterBarNorm(dd[,c("aSize","hge")], xlab="Adult size (m)",
ylab=expression(paste("Height gain efficiency (m ",kg^-1,")")))

## Response variable: heigh gain efficiency (HGE; m/kg)
yy = matrix(,ncol=max(is),nrow=ss)
for(i in 1:nrow(yy)){
  yy[i,1:is[i]] = dd[dd$sp==names(is)[i],"hge"]
}
head(yy)

## Predictor variable: tree adult height (m)
xx = matrix(,ncol=max(is),nrow=ss)
for(i in 1:nrow(xx)){
  xx[i,1:is[i]] = dd[dd$sp==names(is)[i],"aSize"]
}
head(xx)
xx = xx[,1]

### PRIORS
## beta0
aa0 = diff(c(0,10)) # range of possible values for the intercept
tau0 = (4/aa0)^2 # precision of beta0 according to the range method
m0 = aa0/2 # mean of beta0 assumed to be at the center of the range

## beta[i]
taub = tau0 # precision of beta[i] is set to be the same of beta0

## tau[i]
ai = tau0 # minimum allowed value for tau[i] is the same of beta0
bi = 100 # maximum allowed precision for tau[i]
```

```r
## beta1
range(dd$hge) # observed range of HGE
range(dd$aSize) # observed range of adult sizes
aa1 = diff(range(dd$hge))/diff(range(dd$aSize)) # maximum possible value for beta1
tau1 = (4/(2*aa1))^2 # precision of beta1 according to the range method

### JAGS RUN
# Jags input info
data = list(x=xx, y=yy, ss=ss, is=as.numeric(is), # raw data
            taub=taub, ai=ai, bi=bi, m0=m0, tau0=tau0, tau1=tau1) # constants
inits = rep(list(list(
  beta=rep(0,ss), tau=rep(1,ss), # species-specific parameters
  beta0=0, beta1=0 # hyperparameters
)),3) # number of chains
params = c("beta0","beta1","beta","mu","tau")

# Jags output
model.out = jags(data=data, inits=inits, parameter=params, "model.txt",
                 n.chains=3, n.iter=501000, n.burnin=0, n.thin=100, DIC=F)
outparams = dimnames(model.out$BUGSoutput$sims.array)[[3]] # all parameter names estimated by jags

# Take the first 1000 runs as burnin
Output = AddBurnin(model.out$BUGSoutput$sims.array, burnin=1000,n.thin=1)

# Checking for MCMC convergence
par(mfrow=c(2,3))
for(i in c("beta[1]","beta[10]","tau[1]","mu[1]","beta0","beta1")){
  acf(model.out$BUGSoutput$sims.array[1:5000, 1, i], lag.max= 160, main=i)
}
par(mfrow=c(1,1))

# Time series
cols = rainbow(3,alpha=0.7)

par(mfrow=c(3,2),mar=c(1, 4, 4, 2) + 0.1)
for(i in c("beta[1]","beta[10]","tau[1]","mu[1]","beta0","beta1")){
  plot(model.out$BUGSoutput$sims.array[1:1000, 1, i], type="l", col=cols[1], main=i, ylab="",
  xlab="Iteration")
  lines(model.out$BUGSoutput$sims.array[1:1000, 2, i], type="l", col=cols[2])
  lines(model.out$BUGSoutput$sims.array[1:1000, 3, i], type="l", col=cols[3])
}
par(mfrow=c(1,1),mar=c(5, 4, 4, 2) + 0.1)

### RESULTS
## Main results
posts = Output$Burnin.sims.matrix
tab = round(Output$Burnin.Summary,3)[,1:4]
head(tab)

# Table1. Betas
tab1 = tab[c("beta0","beta1",paste("beta[",1:ss,"]",sep="")),]
tab1a = tab1[1:ceiling(nrow(tab1)/2),]
tab1b = rbind(tab1[ceiling(nrow(tab1)/2+1):nrow(tab1),],rep(NA,4))
tab1f = cbind(tab1a,cbind(row.names(tab1b),tab1b))
head(tab1f)
tail(tab1f)
xtable(tab1f)

# Table2. Mus
tab2 = tab[paste("mu[",1:ss,"]",sep=""),]
tab2a = tab2[1:ceiling(nrow(tab2)/2),]
tab2b = rbind(tab2[ceiling(nrow(tab2)/2+1):nrow(tab2),],rep(NA,4))
tab2f = cbind(tab2a,cbind(row.names(tab2b),tab2b))
head(tab2f)
tail(tab2f)
xtable(tab2f)

# Table3. Taus
tab3 = tab[paste("tau[",1:ss,"]",sep=""),]
tab3a = tab3[1:ceiling(nrow(tab3)/2),]
tab3b = rbind(tab3[ceiling(nrow(tab3)/2+1):nrow(tab3),],rep(NA,4))
tab3f = cbind(tab3a,cbind(row.names(tab3b),tab3b))
head(tab3f)
tail(tab3f)
xtable(tab3f)

## Regression parameters
par(mfrow=c(1,2))
plot(density(posts[,"beta0"]),xlab=expression(paste(beta[0])),main="",xlim=c(-1,10))
curve(dnorm(x,m0,sqrt(1/tau0)),add=T,lty=2)
legend(x=4,y=.5,lty=2:1,c("Prior","Posterior"),bty="n")
plot(density(posts[,"beta1"]),xlab=expression(paste(beta[1])),main="")
curve(dnorm(x,0,sqrt(1/tau1)),add=T,lty=2)
par(mfrow=c(1,1))

## Species-specific parameters
```

```r
jpeg("spar.jpeg",height=800,quality=100,)
par(mfrow=c(3,1))
boxplot(posts[1:1000,paste("beta[",1:ss,"]",sep="")],range=0,xaxt="n",ylab=expression(paste(beta[i])),
xlab="Species")
abline(h=0,lty=3,col="red")

boxplot(posts[1:1000,paste("mu[",1:ss,"]",sep="")],range=0,xaxt="n",ylab=expression(paste(mu[i])),
xlab="Species")
#abline(h=mean(Output$Burnin.Summary[paste("mu[",1:ss,"]",sep=""),"mu.vect"]),lty=3,col="red")

boxplot(posts[1:1000,paste("tau[",1:ss,"]",sep="")],range=0,xaxt="n",ylab=expression(paste(tau[i])),
xlab="Species")
#abline(h=mean(Output$Burnin.Summary[paste("tau[",1:ss,"]",sep=""),"mu.vect"]),lty=3,col="red")
par(mfrow=c(1,1))
dev.off()

## Singletons
table(is)[1]/sum(table(is))

### SENSITIVITY
senan = function(ni=31000, m0=5, tau0=0.16,
                 tau1=97.97005, ai=0.16, bi=100, taub=0.16){
  data = list(x=xx, y=yy, ss=ss, is=as.numeric(is),
              taub=taub,ai=ai,bi=bi,m0=m0,tau0=tau0,tau1=tau1)
  model.out = jags(data=data, inits=NULL, parameter=params, "model.txt", n.chains=3,
  n.iter=ni, n.burnin=0, n.thin=20, DIC=F)
  Output = AddBurnin(model.out$BUGSoutput$sims.array, burnin=1000,n.thin=20)
  return(list(Output$Burnin.Summary,Output$Burnin.sims.matrix[,"beta1"]))
  }

## Set beta1 prior to be more or less variable
T1m = senan(tau1=tau1/2,ni=101000) # more variable
T1d = senan(tau1=tau1*2,ni=101000) # less variable

## Set beta0 prior to be centered around 0 or -5
M0 = senan(m0=0,ni=101000)
Mn5 = senan(m0=-5,ni=101000)

## Set beta[i] to be more or less variable
Tbm = senan(taub=taub/2,ni=101000)
Tbd = senan(taub=taub*2,ni=101000)

## Set lower limit of tau[i] to be
A001 = senan(ai=0.01,ni=101000)
A50 = senan(ai=50,ni=101000)

## Plot sensitivities of priors parameters on beta1
par(mfrow=c(2,2))
# tau
rr = range(density(posts[,"beta1"])$y,
           density(T1m[[2]])$y,
           density(T1d[[2]])$y)
plot(density(posts[,"beta1"]),xlab="",main=expression(bold(paste(tau))),ylim=rr)
lines(density(T1m[[2]]),lty=2)
lines(density(T1d[[2]]),lty=3)
legend(x=.05,y=11,lty=1:3,c(expression(paste(tau,"_=_98*")),
expression(paste(tau,"_=_49")),expression(paste(tau,"_=_196"))),bty="n",y.intersp=1.5,cex=.8)
# m0
rr = range(density(posts[,"beta1"])$y,
           density(M0[[2]])$y,
           density(Mn5[[2]])$y)
plot(density(posts[,"beta1"]),xlab="",main=expression(bold(paste(m[0]))),ylim=rr)
lines(density(M0[[2]]),lty=2)
lines(density(Mn5[[2]]),lty=3)
legend(x=.05,y=11,lty=1:3,c(expression(paste(m[0],"_=_5*")),
expression(paste(m[0],"_=_0")),expression(paste(m[0],"_=_-5"))),bty="n",y.intersp=1.5,cex=.8)
# taub
rr = range(density(posts[,"beta1"])$y,
           density(Tbm[[2]])$y,
           density(Tbd[[2]])$y)
plot(density(posts[,"beta1"]),xlab="",main=expression(bold(paste(tau[b]))),ylim=rr)
lines(density(Tbm[[2]]),lty=2)
lines(density(Tbd[[2]]),lty=3)
legend(x=.03,y=14,lty=1:3,c(expression(paste(tau[b],"_=_0.16*")),
expression(paste(tau[b],"_=_0.08")),expression(paste(tau[b],"_=_0.32"))),bty="n",y.intersp=1.5,cex=.8)
# a
rr = range(density(posts[,"beta1"])$y,
           density(A001[[2]])$y,
           density(A50[[2]])$y)
plot(density(posts[,"beta1"]),xlab="",main=expression(bold(paste(a))),ylim=rr)
lines(density(A001[[2]]),lty=2)
lines(density(A50[[2]]),lty=3)
legend(x=.03,y=10,lty=1:3,c(expression(paste(a,"_=_0.16*")),
expression(paste(a,"_=_0.01")),expression(paste(a,"_=_0.50"))),bty="n",y.intersp=1.5,cex=.8)

par(mfrow=c(1,1))
```