

1 Supplementary Material: Budburst timing within a functional
2 trait framework

3
4 **Figures & Tables**

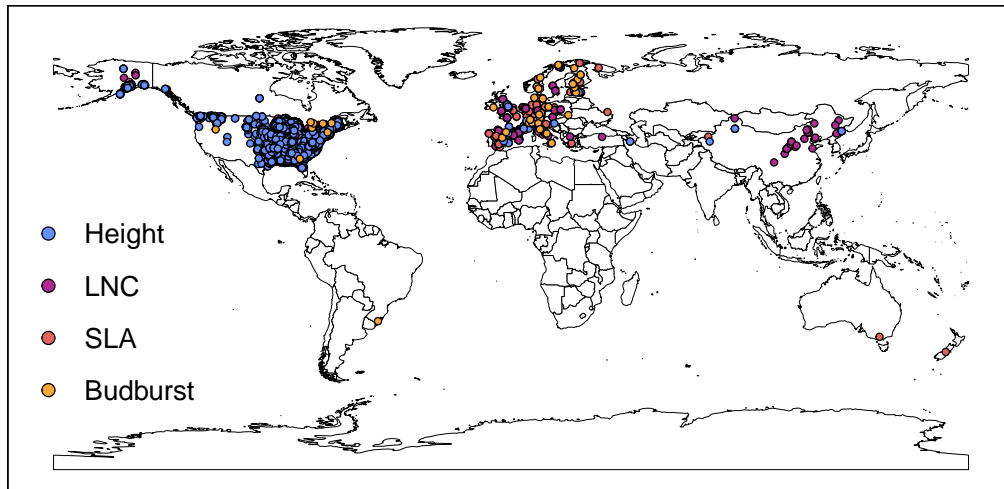


Figure S1: We obtained data from the TRY and BIEN plant trait databases and the OSPREE database of plant phenology experiments for temperate tree species. Following our cleaning of the data and selection of uncorrelated traits, our final dataset included 37 species from 24 unique datasources for the trait data and 34 unique studies for the budburst data. Our data is focused on temperate ecosystems globally with most data originating from North America and Europe.

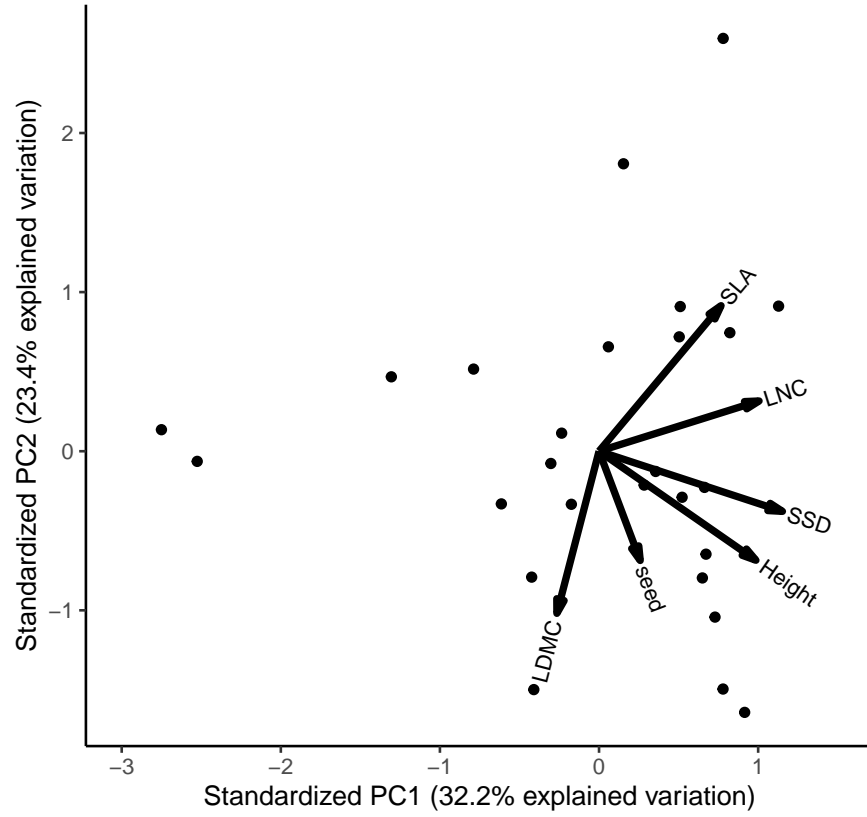


Figure S2: A projection of tree traits across the first and second principle component axis. Arrows represent the direction of vectors for the six functional traits with complete trait data. Points represent the 26 species for which complete trait data was available.

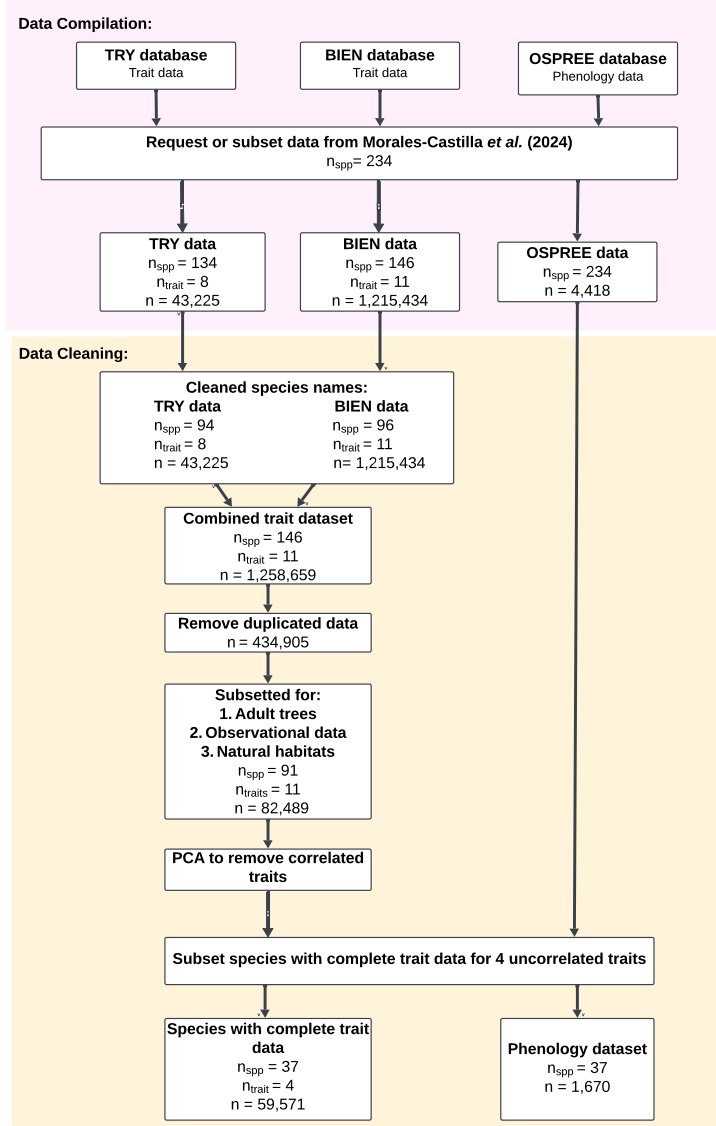


Figure S3: Our initial aim was to include all species from (analyzed by Morales-Castilla *et al.*, 2024), however trait data was only available for a subset of these species. Data was cleaned extensively, with each step depicted by a box, and subset to only include traits for adult trees growing under natural conditions for which we had a complete suite of trait values.

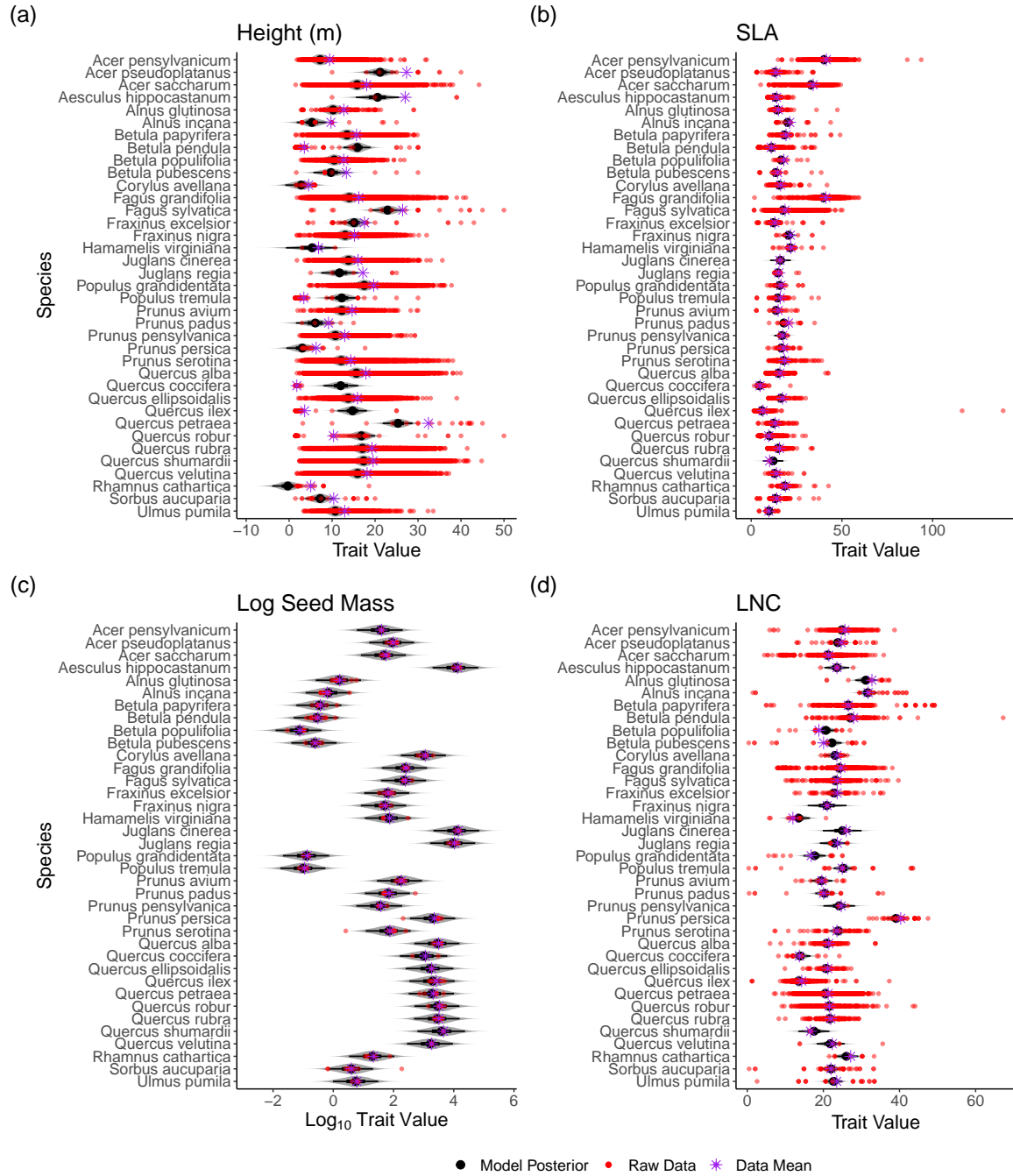


Figure S4: Comparisons of estimated model fits and raw data from joint models of trait effects on budburst phenological cues for 37 species of woody deciduous plants. Four functional traits—(a) height, (b) SLA, (c) seed mass, and (d) LNC—were modeled individually, with the calculated trait value being used to jointly model species' responses to standardized chilling, forcing, and photoperiod cues. Model posteriors are shown in black, with the thicker line depicting the 50% uncertainty interval and the thinner black line the 95% uncertainty interval. Overall species-level model posterior distributions were well-aligned with the raw data, shown in red, and the species-level means from the raw data, denoted as a purple stars.

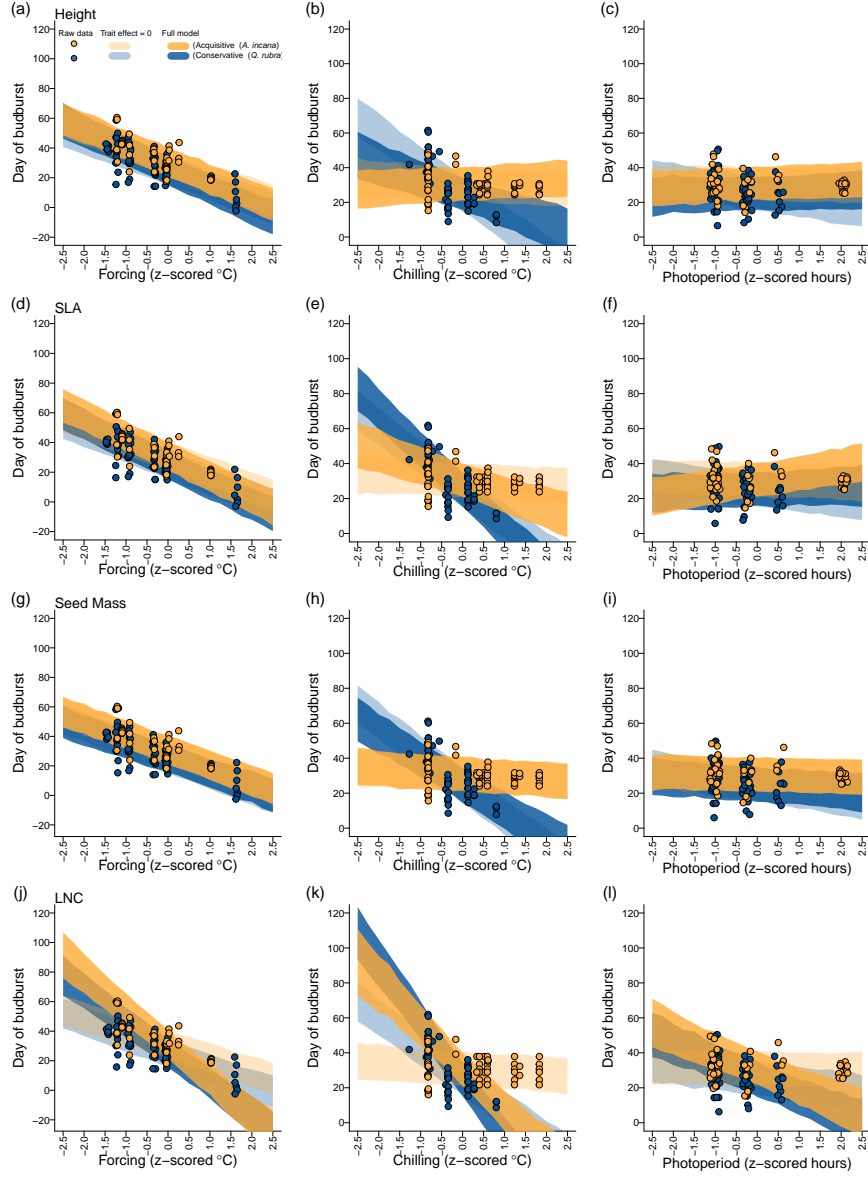


Figure S5: Here we show the relationship between traits and the three phenological cues using as an example an acquisitive species, *Alnus incana* shown in blue, and a conservative species, *Quercus rubra* shown in yellow. The posterior estimates from our height (a-c), SLA (d-f), seed mass (g-i), and LNC (j-l) models were used to estimate the day of budburst for the two species. The effect of height on budburst timing was smallest in response to forcing (a), while the greatest effect of height on budburst was in response to chilling (b), followed by photoperiod (c). The greatest effect of SLA on budburst was only in relation to photoperiod (f). Seed mass had a negligible effect on our estimates budburst (g-i). But LNC had a considerable effect on budburst timing in relation to each cue (j-l). The strength of the relationships can be assessed by comparing the colored bands, with the lighter bands depicting the estimated 50% uncertainty interval without the effect of traits ($\mu_{k,g}$ equal to zero) and darker bands the estimated budburst with the effects of traits included. Points represent the raw budburst data.

Table S1: Bibliographic information for trait data sources from both BIEN and TRY trait databases. Datasets without references or incomplete references are denoted below as ‘unreferenced’.

Database	Reference	Trait name	Unit	No. observations	No. Species
BIEN	Mchugh et al. (2015)	Height	m	26	8
BIEN	Marx et al. (2016)	Height	m	2	2
BIEN	Price et al. (2014)	Height	m	27	19
BIEN	Unreferenced	Height	m	18	16
BIEN	Kleyer et al. (2008)	Height	m	90	19
BIEN	Unreferenced	Height	m	10	10
BIEN	Moles, Angela; unreferenced	Height	m	21	14
BIEN	Reams, Greg; unreferenced	Height	m	47036	19
BIEN	Grime, Hodgson, & Hunt; unreferenced	Height	m	5	5
BIEN	Unreferenced	Height	m	8	5
BIEN	Pérez-de Lis et al. (2017)	Height	m	18	1
BIEN	Robinson et al. (2015)	Height	m	120	1
BIEN	Anderson-teixeira et al. (2015)	Height	m	20	1
TRY	Bond-Lamberty et al. (2002)	Height	m	2	1
TRY	Unpublished	Height	m	275	3
TRY	Wright et al. (2004)	Height	m	28	19
TRY	Prentice et al. (2011)	Height	m	2	2
TRY	Schweingruber and Landolt (2010)	Height	m	21	21
TRY	Unpublished	Height	m	35	2
TRY	Moles et al. (2004)	Height	m	5	5
TRY	Cavender-Bares et al. (2006)	Height	m	1	1
TRY	Diaz et al. (2004)	Height	m	11	10
TRY	Craine et al. (2009)	LNC	mg/g	287	12
TRY	Wilson et al. (2000)	LNC	mg/g	44	2
TRY	Wenxuan et al. (2012)	LNC	mg/g	7	4
TRY	Yahan et al. (2013)	LNC	mg/g	7	3
TRY	Wright et al. (2004)	LNC	mg/g	65	32
TRY	Prentice et al. (2011)	LNC	mg/g	3	2
TRY	Vergutz et al. (2012)	LNC	mg/g	120	20
TRY	Atkin et al. (2015)	LNC	mg/g	24	8
TRY	Marie et al. (2015)	LNC	mg/g	72	22
TRY	Cornelissen et al. (2003)	LNC	mg/g	2	1
TRY	Unpublished	LNC	mg/g	3216	37
TRY	Wang et al. (2017)	LNC	mg/g	6	2
BIEN	Marx et al. (2016)	Seed mass	mg	3	3
BIEN	Unreferenced	Seed mass	mg	4	2
BIEN	Liu et al. (2018)	Seed mass	mg	250	37
BIEN	Ameztegui et al. (2017)	Seed mass	mg	12	12
BIEN	Paine et al. (2015)	Seed mass	mg	12	7
TRY	Wilson et al. (2000)	SLA	mm ² mg-1	44	2
TRY	Unpublished	SLA	mm ² mg-1	204	3
TRY	Wright et al. (2004)	SLA	mm ² mg-1	93	33
TRY	Prentice et al. (2011)	SLA	mm ² mg-1	2	2
TRY	Kleyer et al. (2008)	SLA	mm ² mg-1	102	18
TRY	Unpublished	SLA	mm ² mg-1	83	2
TRY	Atkin et al. (2015)	SLA	mm ² mg-1	40	11
TRY	Marie et al. (2015)	SLA	mm ² mg-1	86	23
TRY	Cornelissen et al. (2003)	SLA	mm ² mg-1	615	14
TRY	Unpublished	SLA	mm ² mg-1	6307	37
TRY	Wang et al. (2017)	SLA	mm ² mg-1	6	2
TRY	Shipley and Vu (2002)	SLA	mm ² mg-1	20	2
TRY	Cavender-Bares et al. (2006)	SLA	mm ² mg-1	42	2
TRY	Unpublished	SLA	mm ² mg-1	1	1
TRY	Diaz et al. (2004)	SLA	mm ² mg-1	11	10

Table S2: Summary of estimates from our model of height ($n = 42781$) using data from 37 focal species. Values represent the mean estimate for model parameters as well as the 50% and 90% uncertainty interval (UI). The strength of the relationship can be assessed by comparing across UI, with parameters with intervals that cross zero depicting weak relationships

	mean	X5.	X25.	X75.	X95.
$\mu_{grand.trait}$	12.7	9.4	11.4	14.0	15.8
$\mu_{k,g}$	32.1	27.8	30.3	33.9	36.5
μ_{force}	-10.7	-15.5	-12.6	-8.8	-6.2
μ_{chill}	-4.1	-10.8	-6.8	-1.4	2.6
μ_{photo}	1.1	-2.6	-0.3	2.5	4.6
$\beta_{trait.force}$	0.2	-0.2	0.0	0.3	0.5
$\beta_{trait.chill}$	-0.5	-1.0	-0.7	-0.3	-0.1
$\beta_{trait.photo}$	-0.2	-0.5	-0.4	-0.1	0.0
$\sigma_{species}$	5.9	4.8	5.4	6.4	7.3
σ_{study}	7.5	5.8	6.7	8.3	9.7
σ_{trait}	5.4	5.4	5.4	5.4	5.4
σ_{pheno}	15.1	11.8	13.8	16.4	18.6
σ_{force}	5.0	3.3	4.1	5.7	7.1
σ_{chill}	8.5	5.6	7.0	9.8	12.4
σ_{photo}	3.2	2.0	2.6	3.8	4.8
σ_d	14.2	13.8	14.0	14.3	14.6

Table S3: Summary of estimates from our model of specific leaf area (SLA, $n = 7656$) using data from 37 focal species. Values represent the mean estimate for model parameters as well as the 50% and 90% uncertainty interval (UI). The strength of the relationship can be assessed by comparing across UI, with parameters with intervals that cross zero depicting weak relationships

	mean	X5.	X25.	X75.	X95.
$\mu_{grand.trait}$	16.8	14.5	15.8	17.8	19.3
$\mu_{k,g}$	31.3	27.2	29.6	33.0	35.6
μ_{force}	-11.4	-16.2	-13.1	-9.6	-7.2
μ_{chill}	-16.7	-24.6	-19.8	-13.3	-9.1
μ_{photo}	1.9	-2.4	0.2	3.6	5.8
$\beta_{trait.force}$	0.2	-0.1	0.1	0.3	0.4
$\beta_{trait.chill}$	0.3	-0.1	0.2	0.5	0.7
$\beta_{trait.photo}$	-0.2	-0.5	-0.3	-0.1	0.0
$\sigma_{species}$	7.8	6.4	7.1	8.4	9.4
σ_{study}	3.3	2.0	2.6	3.8	5.1
σ_{trait}	6.2	6.1	6.1	6.2	6.3
σ_{pheno}	13.9	10.7	12.4	15.3	17.6
σ_{force}	5.0	3.3	4.2	5.6	7.0
σ_{chill}	10.6	7.2	8.9	12.0	14.8
σ_{photo}	3.5	2.3	2.9	3.9	5.0
σ_d	14.2	13.8	14.0	14.3	14.6

Table S4: Summary of estimates from our model of seed mass ($n = 281$) using data from 37 focal species. Values represent the mean estimate for model parameters as well as the 50% and 90% uncertainty interval (UI). The strength of the relationship can be assessed by comparing across UI, with parameters with intervals that cross zero depicting weak relationships

	mean	X5.	X25.	X75.	X95.
$\mu_{grand.trait}$	1.9	1.0	1.5	2.2	2.7
$\mu_{k,g}$	31.4	27.1	29.6	33.1	35.8
μ_{force}	-8.2	-10.8	-9.2	-7.1	-5.6
μ_{chill}	-9.4	-14.0	-11.2	-7.5	-4.8
μ_{photo}	-1.3	-3.4	-2.1	-0.4	0.8
$\beta_{trait.force}$	-0.3	-1.4	-0.8	0.1	0.9
$\beta_{trait.chill}$	-1.1	-2.9	-1.8	-0.4	0.7
$\beta_{trait.photo}$	-0.6	-1.5	-0.9	-0.2	0.4
$\sigma_{species}$	1.6	1.3	1.5	1.7	2.0
σ_{study}	1.0	0.8	0.9	1.0	1.1
σ_{trait}	0.2	0.2	0.2	0.3	0.3
σ_{pheno}	14.8	11.2	13.3	16.3	18.6
σ_{force}	4.9	3.4	4.2	5.5	6.7
σ_{chill}	10.7	7.1	8.8	12.1	15.4
σ_{photo}	3.6	2.3	3.0	4.1	5.1
σ_d	14.1	13.7	14.0	14.3	14.5

Table S5: Summary of estimates from our model of leaf nitrogen content (LNC, $n = 3853$) using data from 37 focal species. Values represent the mean estimate for model parameters as well as the 50% and 90% uncertainty interval (UI). The strength of the relationship can be assessed by comparing across UI, with parameters with intervals that cross zero depicting weak relationships

	mean	X5.	X25.	X75.	X95.
$\mu_{grand.trait}$	22.6	20.4	21.7	23.5	24.9
$\mu_{k,g}$	31.1	27.1	29.4	32.8	35.3
μ_{force}	-19.3	-27.9	-22.9	-15.8	-10.5
μ_{chill}	-27.1	-38.5	-31.7	-22.4	-15.4
μ_{photo}	-9.4	-17.0	-12.5	-6.2	-1.9
$\beta_{trait.force}$	0.5	0.1	0.3	0.6	0.8
$\beta_{trait.chill}$	0.7	0.2	0.5	0.9	1.2
$\beta_{trait.photo}$	0.3	0.0	0.2	0.4	0.6
$\sigma_{species}$	5.1	4.2	4.7	5.5	6.2
σ_{study}	3.6	2.2	2.9	4.1	5.3
σ_{trait}	5.1	5.0	5.1	5.2	5.2
σ_{pheno}	14.0	10.9	12.7	15.3	17.4
σ_{force}	4.6	3.0	3.8	5.2	6.6
σ_{chill}	8.9	6.1	7.5	10.1	12.5
σ_{photo}	3.6	2.4	3.0	4.1	5.0
σ_d	14.2	13.8	14.0	14.3	14.6

5 Stan model code

```

6
7 data {
8   int<lower = 1> n_spec;
9   int<lower = 1> N;
10  int<lower = 1, upper = n_spec> trait_species[N];
11  int<lower = 1> n_study;
12  int<lower = 1, upper = n_study> study[N];
13  vector[N] yTraiti;
14
15  int<lower = 1> Nph;
16  int<lower = 1, upper = n_spec> phenology_species[Nph];
17  vector[Nph] yPhenoi;
18  vector[Nph] forcei;
19  vector[Nph] chilli;
20  vector[Nph] photoi;
21 }
22
23 parameters{
24
25   real mu_grand;
26   vector[n_spec] muSp;
27   vector[n_study] muStudy;
28   real<lower = 0> sigma_traity;
29   real<lower = 0> sigma_sp;
30   real<lower = 0> sigma_study;
31
32   real alphaForceSp[n_spec];
33   real muForceSp;
34   real<lower = 0> sigmaForceSp;
35   real alphaChillSp[n_spec];
36   real muChillSp;
37   real<lower = 0> sigmaChillSp;
38   real alphaPhotoSp[n_spec];
39   real muPhotoSp;
40   real<lower = 0> sigmaPhotoSp;
41   real alphaPhenoSp[n_spec];
42   real muPhenoSp;
43   real<lower = 0> sigmaPhenoSp;
44   real betaTraitxForce;
45   real betaTraitxChill;
46   real betaTraitxPhoto;
47   real<lower = 0> sigmapheno_y;
48 }
49
50 transformed parameters{
51
52   vector[N] y_hat;
53   vector[n_spec] mu_grand_sp;
54
55   real betaForceSp[n_spec];

```

```

56   real betaPhotoSp[n_spec];
57   real betaChillSp[n_spec];
58
59   for(i in 1:n_spec){
60     mu_grand_sp[i] = mu_grand + muSp[i];
61   }
62   for (i in 1:N){
63     y_hat[i] = mu_grand + muSp[trait_species[i]] + muStudy[study[i]];
64   }
65
66   for (isp in 1:n_spec){
67     betaForceSp[isp] = alphaForceSp[isp] + betaTraitxForce * (mu_grand_sp[isp]);
68   }
69   for (isp in 1:n_spec){
70     betaPhotoSp[isp] = alphaPhotoSp[isp] + betaTraitxPhoto * (mu_grand_sp[isp]);
71   }
72   for (isp in 1:n_spec){
73     betaChillSp[isp] = alphaChillSp[isp] + betaTraitxChill * (mu_grand_sp[isp]);
74   }
75 }
76
77 model{
78   yTraiti ~ normal(y_hat, sigma_traity);
79   muSp ~ normal(0, sigma_sp);
80   muStudy ~ normal(0, sigma_study);
81   mu_grand ~ normal(20,10);
82   sigma_sp ~ normal(4,5);
83   sigma_study ~ normal(2,5);
84   sigma_traity ~ normal(3,5);
85
86   for (i in 1:Nph){
87     yPhenoi[i] ~ normal(alphaPhenoSp[phenology_species[i]] +
88       betaForceSp[phenology_species[i]] * forcei[i] +
89       betaPhotoSp[phenology_species[i]] * photoi[i] +
90       betaChillSp[phenology_species[i]] * chilli[i],
91       sigmapheno_y);
92   }
93
94   alphaPhenoSp ~ normal(muPhenoSp, sigmaPhenoSp);
95   alphaForceSp ~ normal(muForceSp, sigmaForceSp);
96   alphaChillSp ~ normal(muChillSp, sigmaChillSp);
97   alphaPhotoSp ~ normal(muPhotoSp, sigmaPhotoSp);
98
99   muPhenoSp ~ normal(40,10);
100  sigmaPhenoSp ~ normal(5,5);
101
102  sigmapheno_y ~ normal(10,5);
103
104  muForceSp ~ normal(-15,10);
105  sigmaForceSp ~ normal(5,5);
106
107  muChillSp ~ normal(-15,10);

```

```

108     sigmaChillSp ~ normal(5,5);
109
110     muPhotoSp ~ normal(-15,10);
111     sigmaPhotoSp ~ normal(5,5);
112
113     betaTraitxForce ~ normal(0,1);
114     betaTraitxPhoto ~ normal(0,1);
115     betaTraitxChill ~ normal(0,1);
116
117 }
118

```

References

- Ameztegui, A., A. Paquette, B. Shipley, M. Heym, C. Messier, and D. Gravel. 2017. Shade tolerance and the functional trait : demography relationship in temperate and boreal forests. *Functional Ecology* 31:821–830.
- Anderson-teixeira, K. J., J. C. Mcgarvey, H. C. Muller-landau, J. Y. Park, E. B. Gonzalez-akre, V. Herrmann, A. C. Bennett, C. V. So, N. A. Bourg, J. R. Thompson, S. M. McMahon, and W. J. Mcshea. 2015. Size-related scaling of tree form and function in a mixed-age forest. *Functional Ecology* 29:1587–1602.
- Atkin, O., K. Bloomfield, P. Reich, M. Tjoelker, G. Asner, D. Bonal, G. Bönisch, M. Bradford, L. Cernusak, E. Cosio, D. Creek, C. K.Y., T. Domingues, J. Dukes, J. Egerton, J. Evans, G. Farquhar, N. Fyllas, P. Gauthier, E. Gloor, T. Gimeno, K. Griffin, R. Guerrieri, M. Heskell, C. Huntingford, F. Ishida, J. Kattge, H. Lambers, M. Liddell, J. Lloyd, C. Lusk, R. Martin, A. Maksimov, T. Maximov, Y. Malhi, B. Medlyn, P. Meir, L. Mercado, N. Mirotchnick, D. Ng, Ü. Niinemets, O. O’Sullivan, O. Phillips, L. Poorter, P. Poot, I. Prentice, N. Salinas, L. Rowland, M. Ryan, S. Sitch, M. Slot, N. Smith, M. Turnbull, M. VanderWel, F. Valladares, E. Veneklaas, L. Weerasinghe, C. Wirth, I. Wright, K. Wythers, J. Xiang, S. Xiang, and J. Zaragoza-Castells. 2015. Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist* 206:614–636.
- Bond-Lamberty, B., C. Wang, and S. T. Gower. 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. *Canadian Journal of Forest Research* 32:1441–1450.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:109–122.
- Cornelissen, J. H. C., B. Cerabolini, P. Castro-Diez, P. Villar-Salvador, G. Montserrat-Marti, J. P. Puyravaud, M. Maestro, M. J. A. Werger, and R. Aerts. 2003. Functional traits of woody plants: correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science* 14:311–322.
- Craine, J. M., A. J. Elmore, M. P. M. Aidar, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, M. C. Mack, K. K. Mclauchlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, J. Penuelas, P. B. Reich, E. A. G. Schuur, W. D. Stock, P. H. Templer, R. A. Virginia, J. M. Welker, and I. J. Wright. 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* 183:980–992.
- Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Diez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M. C. Pérez-Rontomé, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martinez, A. Romo-Diez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems : Evidence from three continents. *Journal of Vegetation Science* 15:295–304.
- Kleyer, M., R. M. Bekker, I. C. Knevel, J. P. Bakker, K. Thompson, M. Sonnenschein, P. Poschlod, J. M. V. Groenendaal, L. Klime, J. Klimesova, S. Klotz, G. M. Rusch, M. Hermy, D. Adriaens, G. Boedeltje, B. Bossuyt, A. Dannemann, P. Endels, L. Götzenberger, J. G. Hodgson, A.-k. Jackel, I. Kühn, D. Kunzmann, W. A. Ozinga, C. Römermann, M. Stadler, J. Schlegelmilch, H. J. Steendam, O. Tackenberg, B. Wilmann, J. H. C. Cornelissen, O. Eriksson, E. Garnier, and B. Peco. 2008. The LEDA Traitbase : a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96:1266–1274.

166 Liu, K., S. Eastwood, R.J. a d Flynn, R. Turner, and W. Stuppy. 2018. Kew database.

167 Marie, V., I. J. Wright, I. C. Prentice, N. H. Batjes, R. Bhaskar, P. M. van Bodegom, W. K. Cornwell,
168 D. Ellsworth, Ü. Niinemets, A. Ordonez, P. B. Reich, and L. S. Santiago. 2015. Global effects of soil
169 and climate on leaf photosynthetic traits and rates. *Global Ecology and Biogeography* 24:706–717.

170 Marx, H. E., D. E. Giblin, P. W. Dunwiddie, and D. C. Tank. 2016. Deconstructing Darwin’ s
171 Naturalization using community phylogenetics and functional traits. *Diversity and Distributions*
172 22:318–331.

173 Mchugh, N., J. L. Edmondson, K. J. Gaston, J. R. Leake, and O. S. O. Sullivan. 2015. Modelling
174 short-rotation coppice and tree planting for urban carbon management – a citywide analysis. *Journal*
175 *of Applied Ecology* 52:1237–1245.

176 Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species produce
177 more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of*
178 *Ecology* 92:384–396.

179 Paine, C. E. T., L. Amissah, H. Auge, C. Baraloto, M. Baruffol, N. Bourland, H. Bruelheide, K. Dainou,
180 R. C. de Gouvenain, J.-l. Doucet, S. Doust, P. V. A. Fine, C. Fortunel, J. Haase, K. D. Holl, H. Jac-
181 tel, X. Li, K. Kitajima, J. Koricheva, C. Martínez-Garza, C. Messier, A. Paquette, C. Philipson,
182 D. Piotto, L. Poorter, J. M. Posada, C. Potvin, K. Rainio, S. E. Russo, M. Ruiz-jaen, M. Scherer-
183 lorenzen, C. O. Webb, S. J. Wright, R. A. Zahawi, and A. Hector. 2015. Globally , functional
184 traits are weak predictors of juvenile tree growth , and we do not know why. *Journal of Ecology*
185 103:978–989.

186 Pérez-de Lis, G., J. M. Olano, V. Rozas, S. Rossi, R. A. Vázquez-Ruiz, and I. García-Gonzalez. 2017.
187 Environmental conditions and vascular cambium regulate carbon allocation to xylem growth in
188 deciduous oaks. *Functional Ecology* 31:592–603.

189 Prentice, I. C., T. Meng, H. Wang, S. P. Harrison, J. Ni, and G. Wang. 2011. Evidence of a universal
190 scaling relationship for leaf CO₂ drawdown along an aridity gradient. *New Phytologist* 190:169–180.

191 Price, C. A., I. J. Wright, D. D. Ackerly, Ü. Niinemets, P. B. Reich, and E. J. Veneklaas. 2014. Are
192 leaf functional traits ‘invariant’ with plant size and what is ‘invariance’ anyway? *Functional Ecology*
193 28:1330–1343.

194 Robinson, K. M., C. Hauzy, N. Loeuille, and B. R. Albrechtsen. 2015. Relative impacts of environmental
195 variation and evolutionary history on the nestedness and modularity of tree–herbivore networks.
196 *Ecology and Evolution* 5:2898–2915.

197 Schweingruber, F., and W. Landolt. 2010. The xylem database.

198 Shipley, B., and T.-T. Vu. 2002. Dry matter content as a measure of dry matter concentration in
199 plants and their parts. *New Phytologist* 153:359–364.

200 Vergutz, L., S. Manzoni, A. Porporato, R. Novais, and R. Jackson. 2012. A Global Database of
201 Carbon and Nutrient Concentrations of Green and Senesced Leaves. Oak Ridge National Laboratory
202 Distributed Active Archive Center Oak Ridge, Tennessee, U.S.A.

203 Wang, H., S. P. Harrison, I. C. Prentice, Y. Yang, F. Bai, H. Furstenua Togashi, M. Wang, S. Zhou,
204 and J. Ni. 2017. The China Plant Trait Database. PANGAEA .

205 Wenxuan, H., C. Yahan, Z. Fang-Jie, L. Tang, J. Rongfeng, and Z. Fusuo. 2012. Floral, climatic and
206 soil pH controls on leaf ash content in China’s terrestrial plants. *Global Ecology and Biogeography*
207 21:376–382.

- 208 Wilson, K. B., D. D. Baldocchi, and P. J. Hanson. 2000. Spatial and seasonal variability of photo-
 209 synthetic parameters and their relationship to leaf nitrogen in a deciduous forest. *Tree Physiology*
 210 20:565–578.
- 211 Wright, I. J., M. Westoby, P. B. Reich, J. Oleksyn, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-
 212 Bares, T. Chapin, J. H. C. Cornellissen, M. Diemer, J. Flexas, J. Gulias, E. Garnier, M. L. Navas,
 213 C. Roumet, P. K. Groom, B. B. Lamont, K. Hikosaka, T. Lee, W. Lee, C. Lusk, J. J. Midgley,
 214 Ü. Niinemets, H. Osada, H. Poorter, P. Pool, E. J. Veneklaas, L. Prior, V. I. Pyankov, S. C.
 215 Thomas, M. G. Tjoelker, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature*
 216 428:821–827.
- 217 Yahan, C., H. Wenxuan, T. Luying, T. Zhiyao, and F. Jingyun. 2013. Leaf nitrogen and phosphorus
 218 concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography*
 219 36:178–184.