1	Electronic Supplementary Material
2	
3	Details of methodology and analyses
4	(a) Literature search
5	We searched for relevant data on SciVerse Scopus database using the following series of
6	related combinations of terms for herbivory:
7	TITLE-ABS-KEY("rate* of grazing" OR "grazing rate" OR "amount of grazing" OR "level*
8	of grazing" OR "grazing level*" OR "rate* of herbivor*" OR "herbivor* rate" OR "amount of
9	herbivor*" OR "herbivory level*" OR "level* of herbivory" OR "degree of herbivor*" OR
10	"rate* of defoliat*" OR "defoliat* rate" OR "amount of defoliat*" OR "defoliation level*" OR
11	"level* of defoliation" OR "foli* damage*" OR "foli* level*" OR "level* of foli*" OR "leaf
12	min* damag*" OR "leaf area remov*" OR "leaf damage" OR "damage to lea*" OR "percent
13	leaf area" OR "leaf area damage" OR "removal of leaf" OR "leaf consumption" OR
14	"consumption of leaves" OR "leaf herbivor*" OR "canopy consumption" OR "consumption of
15	canopy" OR "canopy damag*" OR "canopy defoliation" OR "foliage damag*" OR "foliage
16	consum*" OR "consumption of foliage" AND NOT *plankton* AND NOT alga*) AND
17	DOCTYPE(ar OR ip OR cp OR le OR no OR sh)
18	* Truncated words with all possible ending will be identified
19	
20	(b) Data selection criteria
21	In collecting data our aim was to obtain measurements of leaf herbivory that were comparable

across all plant species and ecosystems. We therefore only retained data that was likely to

represent the amount of natural herbivory that a typical leaf from a given species would experience

24 in a single year. We excluded studies or treatments within studies that added herbivores to plants. In order to conduct a phylogenetically explicit analysis we focused on species-level estimates. 25 Finally, we excluded studies that only reported leaf herbivory during an outbreak year without 26 baseline data because these extreme events do not represent natural herbivory rates unless 27 corrected for frequency of occurrence. One caveat to our method is that our estimates of herbivory 28 might be lower than historical averages if taxa that acted as major herbivores in the past recently 29 went extinct. This might be especially true for some large grassland herbivores (e.g., Bison) and 30 other megafauna (e.g., Moa, Woolly Mammoth and Giant Sloth), which were hunted to extinction 31 32 or functionally removed from their native ecosystems. Even so, our estimates should accurately reflect modern rates of herbivory and the loss of these herbivores should not affect our ability to 33 make inferences about evolutionary differences in herbivory and defence among plant lineages. 34 35 We focused on damage to leaf tissue for multiple reasons. First, leaf herbivory has strong 36 impacts on individual plants and communities [1-3]. Studies show that even small amounts of leaf 37 herbivory can reduce plant fitness [4, 5]. Although herbivory can cause variable impacts on plant 38 growth, recent meta-analyses of experimental studies find that aboveground leaf herbivory 39 frequently causes reduced plant growth, photosynthesis, and fitness compared to protected plants with effects as large as competition between plants [6, 7]. Leaf herbivory has also been shown to 40 41 influence the evolution of defensive traits [8-10], plant population dynamics [3], species distributions and community composition [3, 11], and ecosystem productivity [12-14]. Second, 42 quantifying leaf damage is easier and thus much more common than quantifying damage on roots, 43 reproductive tissues, or damage caused by piercing herbivores [15, 16]. For example, damage 44 caused by phloem feeders might only be apparent if one quantifies the loss of growth potential 45 compared to undamaged plants. Third, leaf damage is easier to standardize across species since 46 leaves are almost always present in the growing season, unlike some other tissues [e.g., flowers 47

and fruits; 17]. It is difficult to say whether damage to leaves is representative of other tissues 48 because few studies have compared damage rates directly [18]. The few studies that have made 49 such comparisons suggest that leaf herbivory is usually higher than root herbivory and similar to 50 or lower than damage to flowers and fruits [17, 19]. Fourth, we focused on percent leaf area lost 51 caused by chewing, grazing, leaf mining, and scraping but excluded damage due to galling, 52 phloem and xylem feeding because quantifying tissue loss due to these processes is difficult to do 53 across many species [15, 16, 20]. The study of herbivory at the scale we present here, both in 54 phylogenetic breadth and number of species, is currently only possible using percent leaf area 55 56 damage.

To effectively compare rates of leaf herbivory across species we collected estimates of 57 annual percent damage. In deciduous species, the limited growing season limits leaf life-span to a 58 59 single year and measures collected towards the end of the growing season accurately reflect annual rates of damage [20]. In evergreen species, leaves can survive for multiple years, which could 60 61 cause an overestimation of annual damage. This is probably a minor effect because most damage 62 to leaves occurs within their first year [21]. A more complex issue occurs in species that continually produce new leaves because annual rates of herbivory will depend on the rate of leaf 63 production. This issue has motivated researchers to present herbivory as a daily rate of damage 64 65 usually measured over several months with regular sampling [22, 23]. These values are not easily converted into annual leaf herbivory because rates of damage change with leaf age and season. 66 One cannot simply sum daily rates of damage over a year, which can reach over 100% [22], 67 without correcting for leaf production and [the number of leaf flushes; 24]. Given these 68 limitations, our approach for this type of data was to estimate total herbivory received by a leaf 69 during its lifetime, most of which occurs within its first year of growth as an estimate of the 70 proportion of annual primary production consumed (see below). 71

72 The various methodologies used to measure percent leaf herbivory have received much attention [20-22, 25]. The two most common sampling approaches are: i) single measures of 73 herbivory on standing leaves, and ii) the quantification of herbivory on marked leaves over an 74 extended period of time. Both methods have potential shortcomings. Standing measures of 75 herbivory can underestimate annual herbivory when completely consumed leaves are not 76 measured [20, 22, 25-27]. The marking approach can overestimate damage when missing leaves 77 are assumed to have been completely consumed when in fact some leaves might have been 78 dropped by the plant after a smaller amount of damage [20, 28]. In addition, marking leaves can 79 80 alter rates of herbivory because repeated human visitation can increase rates of herbivory for some species [29, 30]. 81

We included data collected using both the standing and marked methods. This was justified 82 83 because standing measures of leaf herbivory are the most commonly reported and often the only available data for most species. Furthermore, some authors do account for completely consumed 84 leaves by looking for evidence of chewing damage on petioles [31-33]. Most studies however, do 85 86 not explicitly state how they deal with missing leaves and others reveal that it was impossible to 87 determine the cause of damage even with careful observation [20]. However, when both types of data were available, we used that from marked leaves, assuming the total damage received at the 88 end of the sampling period as a measure of annual herbivory. Details of the studies included in the 89 database, including habitat, location, climate, and sampling methodology, can be found in Turcotte 90 et al. [34]. 91

To account for potential methodological biases, we created two datasets of different stringency. In temperate systems, studies that reported herbivory at the end of the summer or fall were included in the stringent dataset whereas a less-stringent dataset also included measurements made in mid-summer (7 studies, data on 22 species). In tropical systems we excluded studies that

96	measured herbivory only during the first month of growth of new leaves. We did so because for
97	most species this period represents an underestimate of annual herbivory; Coley and Barone [21]
98	report that 68%, 47%, and 29% of damage occurs during leaf expansion of species found in
99	tropical wet forests (shade-tolerant species), tropical wet forests (gap specialists), and tropical dry
100	forests, respectively. For tropical systems, we only included data on mature leaves (standing or
101	marked measures) in the stringent dataset. In the less stringent dataset we also included studies of
102	young and old leaves, or of an unknown mixture of leaves (13 studies, 104 species), plus studies
103	measuring herbivory on leaves that were two months old (2 studies, 22 species).
104	Leaf herbivory values were often extracted directly from figures using Web Plot Digitizer
105	(http://arohatgi.info/WebPlotDigitizer/). We also took note when studies mentioned the main
106	herbivores but few studies explicitly quantified herbivore visitation rates especially on different
107	plant species. Of the studies that noted the type of damage, 45% report that insects are the main
108	herbivores (32% Lepidoptera, 20% Coleoptera, and 6% Orthoptera), while 5% identify
109	crustaceans, and 4% report vertebrates as the principal consumer. We acknowledge that our
110	selection criteria might exclude the impact of certain herbivores, such as grassland grazers for
111	which herbivory is not commonly studied by measuring percent leaf area damaged.

112

113 (c) Phylogenetic inference

We first created a backbone family-level phylogeny for the 161 families in the database using the Phylomatic v.3 online tool based on the APG megatree [http://phylodiversity.net/phylomatic; 35]. Species were then added to the tree as polytomies using currently accepted taxonomy [e.g., 36]. We resolved this tree to the species level based on published plastid *rbcL* sequence from NCBI's GenBank (www.ncbi.nlm.nih.gov/genbank), which was available for 487 out of 1058

species. For another 202 species we were able to obtain sequence data from congeners (hereafter"placeholder" species).

We aligned sequences using BioEdit v.7.1.3 [37] and excluded sequences shorter than 500 121 nucleotides. Using the family-level tree as a constraint we reconstructed phylogenetic relationships 122 using maximum likelihood (ML) assuming a general time reversible model with 25 rate categories 123 in RAxML v7.3.1 [38, 39]. We made the branch lengths of the tree proportional to time using 124 Pathd8 v1.0 (http://www2.math.su.se/PATHd8/) and fossil calibrations (table S2). Finally, we 125 generated a posterior distribution of dated trees using BEAST v1.7.4 [http://beast.bio.ed.ac.uk; 126 127 40], using the ML topology as a constraint and allowing branch lengths to vary assuming a general time reversible model of DNA evolution, as selected as the best fit model by jModelTest v2.1.1 128 [41]. We used a log-normal relaxed clock to estimate substitution rate variation and time calibrated 129 130 the analysis using 19 fossil dates (table S2) as log-normal priors. We ran six BEAST analyses each lasting 33 to 72 million generations, where the first 8 to 15 million generations were discarded as 131 132 burn-in. Each of the separate post-burn-in runs was then concatenated, and the maximum clade 133 credibility values were extracted using TreeAnnotator. Phylogenetic inference was conducted on CIPRES (www.phylo.org). 134 Species for which no sequence data was available (367 species) were included as polytomies at 135

the least inclusive node, mostly at the level of genus, although 27 species had to be added at their
family node (the Nexus formatted script of the unresolved phylogeny is available as a
supplementary material). We then resolved polytomies using a Bayesian approach that fits a birth-

death diversification model, generating 1000 fully resolved trees [42].

140

141 (d) Phylogenetic comparative analysis

We used phylogenetic comparative methods to analyse differences in leaf herbivory across plant taxa and to characterize the evolutionary model that best explained variation in herbivory across lineages of vascular plants. First, we assessed the fit of a Brownian Motion (BM) model of stochastic evolution (Equation 1);

146

$$dX(t) = \sigma dB(t) \tag{1}$$

This equation describes the amount of change in trait (X) over a short time period (t). The term (dB(t)) are normal random variables with a mean of zero and variance of ($\sigma^2 dt$). The rate of stochastic evolution is thus (σ^2)[43, 44]. Second, we compared the fit of the Hansen model [45, 46] that assumes an Ornstein-Uhlenbeck (OU) process in which traits evolve toward an evolutionary optimum in a way that is consistent with evolution by stabilizing selection, while genetic drift causes traits to evolve away from this optima in a stochastic manner [43, 44]. This model is represented by equation 2:

154

$$dX(t) = \alpha \left[\theta - X(t)\right]dt + \sigma dB(t)$$
⁽²⁾

155 The additional term represents stabilizing selection, where (α) is the strength of selection 156 pulling the trait value towards the optimum trait value (θ).

157 We compared the fit of alternative models using sample-size corrected Akaike information criteria (AICc) scores [47]. First we compared the fit of simple OU and BM models ('OU1' and 158 159 'BM1') where all branches in the phylogeny had a fixed evolutionary optimum (θ , OU1 model) and rate of stochastic evolution (σ^2 , OU1 and BM1 models). Second, we allowed evolutionary 160 parameters to vary with plant traits. Complex models assumed multiple rates of stochastic 161 162 evolution (BMS) or multiple evolutionary optima (OUM) using the following trait categories: 1) life-history variation – annual, intermediate, and perennial, 2) woodiness – woody and non-woody, 163 and 3) growth form – tree, vine, shrub, graminoid, and forb. Multi-optima and multi-rate models 164 require information on expected trait values for each fitted clade. For this purpose, ancestral state 165

166 estimates were inferred from extant tip data using the *make.simmap* function in *phytools* package [48] in R [49] that simulates stochastic character mapping using a continuous-time reversible 167 Markov chain process. More complex models, that permitted variation in (σ^2) , (θ_i) , and (α) 168 simultaneously [44], would not convergence on stable ML estimates. 169 Analyses were conducted on natural log-transformed leaf herbivory rates (x + 1) using the 170 OUwie v.1.33 package [44] in R v.3.0 [49]. Because large differences in herbivory between major 171 lineages, it was not possible to run complex models across the entire phylogeny, we thus analysed 172 each major taxonomic group separately. Basal angiosperms, basal eudicots, and basal coreeudicots 173 were grouped into a single paraphyletic clade referred to as 'other angiosperms' since these 174 species did not fit as monophyletic groupings with other major lineages (see Fig. 2B for the 175 number of species within each lineage). 176

178 Supplemental tables

- 179 **Table S1.** Mean annual percent leaf tissue consumption as measured by four unpublished studies with taxonomic information and trait
- data. Study (A): data collected by R.M. Godfrey in Trinidad in 2011. Study (B): collected M.T.J. Johnson and G.T. Broadhead in
- 181 Eastern U.S.A. in 2009. Study (C): collected by M.T.J. Johnson in Eastern Canada and U.S.A. in 2012. Study (D): collected by C.J.M.
- 182 Thomsen in Ontario Canada in 2012.

study	species	sunonum	taxonomic	woodinoss	growth	lifa history	mean leaf
study	species	synonym	lineage	wooumess	form	me-mstory	damage (%)
А	Asclepias curassavica		Asterids	Non-Woody	Shrub	Perennial	0.80
A	Bidens pilosa		Asterids	Non-Woody	Forb	Annual	0.40
А	Cassia fruticosa		Rosids	Woody	Tree	Perennial	5.00
А	Chrysothemis pulchella		Asterids	Non-Woody	Forb	Perennial	2.17
A	Lantana camara		Asterids	Woody	Vine	Perennial	5.58
A	Laurentia longiflora	Hippobroma longiflora	Asterids	Non-Woody	Forb	Perennial	0.20

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186

			taxonomic		growth		mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
А	Mimosa pudica		Rosids	Non-Woody	Forb	Intermediate	2.27
A	Psiguria umbrosa	Anguria umbrosa; Citrullus umbrosa	Rosids	Woody	Vine	Perennial	0.67
А	Spermacoce assurgens		Asterids	Non-Woody	Shrub	Intermediate	2.20
A	Stachytarpheta jamaicensis	,	Asterids	Non-Woody	Forb	Intermediate	8.33
A	Trimezia martinicensis		Monocots	Non-Woody	Forb	Perennial	0.20
В	Ambrosia artemisiifolia		Asterids	Non-Woody	Forb	Annual	1.15
В	Aquilegia canadensis		Other Angiosperms	Non-Woody	Forb	Perennial	1.43
В	Asclepias incarnata		Asterids	Non-Woody	Forb	Perennial	0.88
В	Asclepias syriaca		Asterids	Non-Woody	Forb	Perennial	2.68
В	Borrichia frutescens		Asterids	Woody	Shrub	Perennial	0.54
						Table continues	on the next nag

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188

			taxonomic		growth	1.6 1.4	mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
В	Campanula americanum		Asterids	Non-Woody	Forb	Annual	0.73
В	Capsella bursa-pastoris		Rosids	Non-Woody	Forb	Annual	0.10
В	Carduus nutans		Asterids	Non-Woody	Forb	Perennial	7.05
В	Cassia fasciculata		Rosids	Non-Woody	Forb	Annual	3.19
В	Datura stramonium		Asterids	Non-Woody	Forb	Annual	0.24
В	Decodon verticillatus		Rosids	Woody	Shrub	Perennial	1.21
В	Erigeron annuus		Asterids	Non-Woody	Forb	Annual	2.39
В	Hordeum vulgare		Monocots	Non-Woody	Graminoid	Annual	0.00
В	Hypericum perforatum		Rosids	Non-Woody	Forb	Perennial	2.81
В	Impatiens capensis		Asterids	Non-Woody	Forb	Annual	2.01
В	Ipomoea hederacea		Asterids	Non-Woody	Vine	Annual	12.49
В	Ipomoea purpurea		Asterids	Non-Woody	Vine	Annual	3.94
						T 11	7

Table continues on the next page

			taxonomic		growth		mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
В	Juglans nigra		Rosids	Woody	Tree	Perennial	7.78
В	Kalmia latifolia		Asterids	Woody	Shrub	Perennial	1.81
В	Lathyrus latifolius		Rosids	Non-Woody	Vine	Perennial	0.91
В	Liriodendron tulipifera		Magnoliids	Woody	Tree	Perennial	3.90
В	Lobelia cardinalis		Asterids	Non-Woody	Forb	Perennial	1.13
В	Lolium multiflorum		Monocots	Non-Woody	Graminoid	Annual	0.07
В	Mimulus ringens		Asterids	Non-Woody	Forb	Perennial	1.55
В	Oenothera biennis		Rosids	Non-Woody	Forb	Intermediate	6.29
В	Oenothera humifusa		Rosids	Non-Woody	Forb	Perennial	1.10
В	Oenothera laciniata		Rosids	Non-Woody	Forb	Annual	0.56
В	Phlox drummondii		Asterids	Non-Woody	Forb	Annual	0.07
В	Picea rubens		Gymnosperms	Woody	Tree	Perennial	0.00
						Table continues	on the next pag

192

			taxonomic		growth		mean leaf
study	species	species synonym lineage	lineage	woodiness	life-histo form		damage (%)
В	Polystichum acrostichoides		Ferns	Non-Woody	Forb	Perennial	2.31
В	Rhus glabra		Rosids	Woody	Shrub	Perennial	4.55
В	Rhus typhina		Rosids	Woody	Shrub	Perennial	0.75
В	Robinia pseudoacacia		Rosids	Woody	Tree	Perennial	7.34
В	Rumex acetosella		Other Angiosperms	Non-Woody	Forb	Perennial	3.23
В	Rumex hastatulus		Other Angiosperms	Non-Woody	Forb	Perennial	1.82
В	Sabatia angularis		Asterids	Non-Woody	Forb	Annual	4.08
В	Senecio vulgaris		Asterids	Non-Woody	Forb	Annual	2.44
В	Solanum carolinense		Asterids	Non-Woody	Forb	Perennial	3.05
В	Solanum ptychanthum		Asterids	Non-Woody	Forb	Annual	8.86
						Table continues	an the next nee

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			taxonomic		growth	1.0 1.	mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
В	Solidago sempervirens		Asterids	Non-Woody	Forb	Perennial	1.62
В	Spartina alterniflora		Monocots	Non-Woody	Graminoid	Perennial	0.04
В	Taraxacum officinale		Asterids	Non-Woody	Forb	Annual	1.58
В	Trillium erectum		Monocots	Non-Woody	Forb	Perennial	5.23
В	Trillium grandiflorum		Monocots	Non-Woody	Forb	Perennial	0.00
В	Lorinseria areolata	Woodwardia areolata	Ferns	Non-Woody	Forb	Perennial	1.70
В	Yucca filamentosa		Monocots	Woody	Shrub	Perennial	0.11
С	Abies balsamea	Abies balsamifera	Gymnosperms	Woody	Tree	Perennial	3.40
С	Asplenium platyneuron		Ferns	Non-Woody	Forb	Perennial	2.28
C	Brasenia schreberi		Other Angiosperms	Non-Woody	Forb	Perennial	2.36

Table continues on the next page

196

			taxonomic		growth		mean leaf
study	species	species synonym lineage	lineage	woodiness	form	life-history	damage (%)
С	Cystopteris fragilis		Ferns	Non-Woody	Forb	Perennial	6.90
С	Gymnocarpium dryopteris		Ferns	Non-Woody	Forb	Perennial	4.85
С	Juniperus communis		Gymnosperms	Woody	Tree	Perennial	0.30
С	Larix americana		Gymnosperms	Woody	Tree	Perennial	6.52
С	Nuphar variegatum		Other Angiosperms	Non-Woody	Forb	Perennial	6.03
С	Nymphaea odorata		Other Angiosperms	Non-Woody	Forb	Perennial	9.77
С	Osmunda claytoniana		Ferns	Non-Woody	Forb	Perennial	1.30
С	Phegopteris connectilis		Ferns	Non-Woody	Forb	Perennial	11.55
С	Phegopteris dryopteris		Ferns	Non-Woody	Forb	Perennial	1.97
С	Picea glauca		Gymnosperms	Woody	Tree	Perennial	2.03
						Table continue	s on the next near

Table continues on the next page

			taxonomic		growth		mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
С	Picea mariana		Gymnosperms	Woody	Tree	Perennial	0.00
С	Pinus banksiana		Gymnosperms	Woody	Tree	Perennial	0.60
С	Pinus resinosa		Gymnosperms	Woody	Tree	Perennial	4.27
С	Polypodium virginianum		Ferns	Non-Woody	Forb	Perennial	0.74
С	Taxus canadensis		Gymnosperms	Woody	Shrub	Perennial	0.04
С	Thuja occidentalis		Gymnosperms	Woody	Tree	Perennial	1.91
D	Larix laricina		Gymnosperms	Woody	Tree	Perennial	0.60
D	Picea abies		Gymnosperms	Woody	Tree	Perennial	0.06
D	Pinus strobus		Gymnosperms	Woody	Tree	Perennial	0.28
D	Pontederia cordata		Monocots	Non-Woody	Forb	Perennial	1.88
D	Sagittaria latifolia		Monocots	Non-Woody	Forb	Perennial	1.01
D	Tsuga canadensis		Gymnosperms	Woody	Tree	Perennial	0.88

node	year (mya)	node	year (mya)
Lamiales	44.3	Malpighiales	49
Angiosperms	131.0	Myrtales	88.2
Bignoniaceae	35	Pandanales	65.0
Caprifoliaceae	36	Poales	68.1
Caryophyllales	83.5	Proteales	98.0
Cornales	86.0	Sapindales	65
Dilleniaceae	51.9	Solanales	44.3
Ericales	91.2	Vitaceae	57.9
Fabales	59.9	Zingiberales	83.5
Gymnosperms	310		

Table S2. Nineteen fossil ages modelled as log-normal priors. Means of priors were set to 0 with a
standard error of 1 and an offset value as listed in the table [dates were gathered from 50, 51].

203 Supplemental tables

204 Table S3. Comparison of evolutionary model fits for each major lineage. Top values represent median Akaike Information Criterion

- values corrected for sample size (AICc) from comparative analyses performed on the distribution of phylogenetic trees. Below these
- values we report the proportion of trees that show strong support for each model ($\Delta AICc \leq 4$). Models with the strongest support
- 207 ($\Delta AICc \le 4$) are shown in bold. Models include: Brownian Motion models of stochastic evolution with either a single rate of evolution
- 208 (BM1) or multiple rates for different traits (BMS), and Ornstein-Uhlenbeck models of stabilizing selection with either a single
- evolutionary optimum (OU1) or multiple optima for different traits (OUM). Up to three different multi-rate and multi-optima models
- are possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness (woody, non-woody),
- and growth form (tree, shrub, vine, forb, and graminoid). The "other angiosperms" lineage represents a paraphyletic grouping of species
- not contained as monophyletic groups of species in the other major lineages and includes basal angiosperms, basal eudicots, and basal
- 213 coreeudicots.
- 214
- 215
- 216
- 217
- 218
- 219

220 Ta	able S3
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1.	DM1		BMS		011	OUM			
lineage	DIVII	growth form	woodiness	life-history	- 001	growth form	woodiness	life-history	
Forns	106.79				82.56				
rerns	0.045				1.000				
Cumposporms	57.82	•			40.28	•			
Gymnosperms	0.000				1.000				
Magnaliida	89.43	89.91			77.39	79.16			
wragnomus	0.047	0.022			0.992	0.961			
Monocots	474.14	443.58	458.10	474.52	352.95	344.11	354.54	354.19	
Withocots	0.000	0.000	0.000	0.000	0.061	0.923	0.015	0.011	
Rosids	2333.1	2283.77	2307.06	2321.3	1401.5	1400.54	1390.57	1403.4	
KUSIUS	0.000	0.000	0.000	0.000	0.006	0.000	0.810	0.000	
Astorida	1083.7	1026.10	1068.28	1055.1	649.55	638.78	635.41	652.15	
Asterius	0.000	0.000	0.000	0.000	0.001	0.799	0.859	0.000	
Other	338.88	318.27	334.17	337.54	190.55	193.34	188.80	192.96	
Angiosperms	0.000	0.000	0.000	0.000	0.935	0.047	0.937	0.559	

222	Table S4. Parameter estimates for the stabilizing selection models. Maximum likelihood (ML) parameter estimates for each major
223	lineage for the Ornstein-Uhlenbeck models. See table S5 for the parameters of the poorly fitting BM models. Models include the single
224	evolutionary optimum (OU1) and the multiple optima models for different traits (OUM). Up to three different multi-rate models are
225	possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness (woody, non-woody), and
226	growth form (tree, shrub, vine, forb, and graminoid). Estimates are median parameter values of the ML optima value across 1000
227	phylogenetic trees. Values in parentheses are median 95% confidence intervals that were calculated for each tree and thus incorporate
228	both phylogenetic uncertainty and uncertainty in the maximum likelihood estimates. Parameters include the rate of stochastic evolution
229	σ^{2} , the strength of stabilizing selection α , and the ML evolutionary optimum θ , which is a phylogenetically informed estimate of the
230	rate of herbivory for each group [43, 44].
231	
232	
233	
234	
235	
236	
237	
238	

Table S4

linoago		OU1		OUM Life-History						
nneage	α	σ^2	θ	α	σ^2	θ-Annuals	θ – Interm.	θ – Per.		
Ferns	1.13 (1.13- 1.18)	1.7 (0.82-2.64)	5.83 (4.01-8.3)							
Gymnosperms	0.14 (-0.07- 0.36)	0.13 (-0.06-0.33)	0.87 (0.42-1.47)							
Magnoliids	0.09 (-0.05- 0.25)	0.12 (-0.04-0.32)	8.44 (5.47-12.18)	-						
Monocots	1.05 (0.03- 2.64)	3 (0.07-7.2)	3.11 (2.25-4.01)	1.12 (0.03-2.64)	3.37 (0.07-7.14)	1.85 (-0.19-5.26)		3.17 (2.3-4.14)		
Rosids	2.99 (2.99 - 3)	4.58 (4.03-5.2)	8.16 (7.5-8.86)	2.99 (2.99-3)	4.57 (4.02-5.2)	6.61 (3.87-10.8)	5.43 (2.3-11.4)	8.25 (7.57-8.97)		
Asterids	3.21 (3.2-3.25)	5.35 (4.38-6.52)	4.31 (3.73-4.97)	3.2 (3.2-3.25)	5.31 (4.33-6.51)	3.09 (1.48-5.71)	3.75 (2.1-6.3)	4.44 (3.8-5.16)		
Other Angiosperms	2.04 (2.04- 2.06)	3.19 (2.13-4.44)	6.16 (4.8-7.81)	2.03 (2.03-2.06)	3.09 (2.07-4.26)	8.9 (1.94-2.29)	2.05 (-0.15-9.3)	6.27 (4.87-7.98)		

Table continues on the next page

		OUM V	Woodiness	5	OUM Growth Form						
lineage	α	σ^2	θ-Non- Woody	θ- Woody	α	σ^2	θ- Shrub	θ-Tree	θ- Forb	θ-Vine	θ- Graminoid
Ferns											
Gymnosperms	-										
	-				0.16	0.2 (-	12.12	7.58	_		
Magnoliids					(-0.12-	0.13-	(5.75-	(4.77-			
					0.5)	0.6)	23.38)	11.05)			
-	1.2	3.51	2.99	3.77	1.25	2.95	2.43	5.21	5.03	3.07	1.52
Monocots	(0.03-	(0.07-	(2.12-	(1.75-	(0.04-	(0.08-	(0.53-	(2.08-	(3.5-	(0.99-	(0.86-
	2.64)	7.17)	3.94)	6.93)	2.65)	6.24)	6.61)	11.64)	6.94)	6.71)	2.46)
	2.99	4.49	5.48	8.63	2.99	4.54	8.63	8.49	5.97	7.43	
Rosids	(2.99-	(3.95-	(4.28-	(7.9-	(2.99-	(3.99-	(6.82-	(7.7-	(4.58-	(4.92-	
	3)	5.08)	6.94)	9.42)	3)	5.17)	10.85)	9.35)	7.7)	10.94)	
	3.21	5.02	3.08	5.55	3.21	4.99	5.02	5.94	3.02	4.3	-
Asterids	(3.21-	(4.11-	(2.45-	(4.63-	(3.21-	(4.07-	(3.75-	(4.671-	(2.36-	(2.3-	
	3.25)	6.14)	3.83)	6.61)	3.24)	6.07)	6.59)	7.468)	3.79)	7.44)	
Other	2.04	3.01	4.76	7.72	2.04	3.01	7.23	8.21	4.71	8.16	-
Angiosnorms	(2.04-	(2.01-	(3.29-	(5.55-	(2.04-	(2.01-	(4.56-	(4.79-	(3.23-	(2.94-	
Angiosperms	2.06)	4.35)	6.7)	10.55)	2.06)	4.33)	11.09)	13.42)	6.67)	20.4)	

Table S5. Parameter estimates for the stochastic evolution models: Maximum likelihood parameter estimates for each major lineage for the243Brownian Motion models of stochastic evolution with either a single rate of evolution (BM1) or multiple rates for different traits (BMS). Up to three244different multi-optima models are possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness245(woody, non-woody), and growth form (tree, shrub, vine, forb, and graminoid). Estimates are median parameter values of the ML optima value246across 1000 phylogenetic trees. Values in parentheses are median 95% confidence intervals that were calculated for each tree and thus incorporate247both phylogenetic uncertainty and uncertainty in the maximum likelihood estimates. Parameters include the rate of stochastic evolution ' σ^2 ' and the248ML evolutionary optimum ' θ ', which is a phylogenetically informed estimate of the rate of herbivory for each group [43, 44].

]	BM1	BMS Life-History					
lineage	~ ²	Δ	σ^{2-}	σ^{2-}	σ^{2-}	Δ		
	0	0	Annual	Intermediate	Perennial	0		
Forms	0.03	5.52						
rerns	(0.01-0.04)	(-0.74-131.24)						
Cumnasnamms	0.03	0.71	-					
Gymnosperms	(0.01-0.05)	(-0.97-107.03)						
M 1 ¹¹ - 1	0.04	8.78	_					
magnomus	(0.02-0.05)	(0.58-55.47)						
Monocots	0.12	3.61	0.07	-	0.11	3.62		
wonocous	(0.09-0.15)	(-0.78-85.84)	(-0.06-0.22)		(0.08-0.14)	(-0.77-81.7)		
Rosids	0.28	6.71	0.16 (0.02-	0.05	0.27	6.76		
Rosius	(0.24-0.31)	(-0.82-301.21)	0.3)	(-0.05-0.17)	(0.24-0.3)	(-0.8-270.7)		
Asterids	0.23	4.18	0.29	0.4	0.17	4.17		
	(0.19-0.27)	(-0.8-107.64)	(-0.04-0.7)	(0-0.85)	(0.13-0.2)	(-0.69-67.2)		
Other	0.2	6.38	0.001	0.22	0.18	6.42		
Angiosperms	(0.14-0.27)	(-0.97-1451.3)	(-0.002-0.005)	(-0.28-0.76)	(0.12-0.25)	(-0.96-1138.1)		

Table continues on the next page

	BN	IS Woodin	ess	BMS Growth Form						
lineage	σ ²⁻ Non- Woody	σ^{2-} Woody	θ	σ ²⁻ Shrub	σ ²⁻ Tree	σ ²⁻ Forb	σ^{2-} Vine	σ ²⁻ Graminoid	θ	
Ferns										
Gymnosperms										
				0.02	0.04			-	8.89	
Magnoliids				(-0.01-	(0.02-				(0.76-	
				0.06)	0.06)				52.07)	
	0.1	0.11	3.62	0.03	0.14	0.06	0.1	0.1	3.63	
Monocots	(0.07-	(0.03-	(-0.69-	(-0.01-	(0.01-	(0.03-	(-0.01-	(0.06-	(-0.47-	
	0.12)	0.19)	66.6)	0.09)	0.27)	0.08)	0.2)	0.14)	32.37)	
	0.11	0.28	6.58	0.25	0.27	0.11	0.09		6.76	
Rosids	(0.07-	(0.25-	(-0.79 -	(0.12, 0.28)	(0.27)	(0.07-	(0.02-		(-0.68-	
	0.15)	0.32)	247)	(0.13-0.38)	(0.23-0.3)	0.16)	0.17)		190.27	
	0.23	0.16	4.19	0.04	0.17	0.23	0.16		3.96	
Asterids	(0.17-	(0.12-	(-0.67-	0.04	(0.12-	(0.16-	(0.03-		(-0.23-	
	0.3)	0.2)	68.1)	(0.02-0.00)	0.22)	0.29)	0.3)		26.56)	
Other	0.21	0.15	6.4	0.26	0.01	0.2	0.04		6.2	
	(0.11-	(0.08-	(-0.94-	(0.1.0.42)	(-0.00-	(0.11-	(-0.01-		(-0.63-	
Angiosperms	0.31)	0.21)	850)	(0.1-0.42)	0.01)	0.29)	0.09)		128.8)	

254 Supplemental figures

255 Supplemental figure legends

Figure S1. Evolutionary parameters for the best fitting model. Comparison of the evolutionary parameters estimated from the best fitting macroevolutionary model for each major plant lineage. $'\alpha'$ represents the strength of stabilizing selection and $'\sigma^2'$ is the rate of stochastic evolution [43]. Values represent median estimates and median 95% confidence intervals over the distribution of 1000 phylogenies.

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Figure S2. Relationship between herbivory and life-history variation. Percent leaf herbivory for
lineages that vary in life-history strategy, which represent the evolutionary optima from the
stabilizing selection model (OUM – Life-History). Values represent median percent leaf herbivory
and median 95% confidence intervals over the distribution of 1000 phylogenies. Number of
species for each group is found within data points. Annual 'other angiosperms' were poorly
sampled and has a wide 95% confidence interval (1.9% – 32.3%) that extended beyond the bounds
of the figure.

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275 Supplemental References

- [1] Crawley, MJ. 1989 Insect herbivores and plant population dynamics. Annu. Rev. Entomol. 34,
- 277 531-562. (doi:doi:10.1146/annurev.en.34.010189.002531).
- [2] McNaughton, SJ, Oesterheld, M, Frank, DA & Williams, KJ. 1989 Ecosystem-level patterns
- of primary productivity and herbivory in terrestrial habitats. *Nature* **341**, 142-144.
- 280 [3] Maron, JL & Crone, E. 2006 Herbivory: effects on plant abundance, distribution and
- 281 population growth. *Proc. R. Soc. B* 273, 2575-2584. (doi:10.1098/rspb.2006.3587).
- [4] Clark, DB & Clark, DA. 1985 Seedling dynamics of a tropical tree: Impacts of herbivory and
- 283 meristem damage. *Ecology* **66**, 1884-1892.
- [5] Marquis, RJ. 1992 A bite is a bite is a bite? Constraints on response to folivory in *Piper*
- arieianum (Piperaceae). Ecology 73, 143-152.
- [6] Hawkes, CV & Sullivan, JJ. 2001 The impact of herbivory on plants in different resource
- conditions: a meta-analysis. *Ecology* **82**, 2045-2058.
- [7] Bigger, DS & Marvier, MA. 1998 How different would a world without herbivory be?: A
 search for generality in ecology. *Integr. Biol.* 1, 60-67.
- [8] Turley, NE, Odell, WC, Schaefer, H, Everwand, G, Crawley, MJ & Johnson, MTJ. 2013
- 291 Contemporary evolution of plant growth rate following experimental removal of herbivores. *Am.*
- 292 *Nat.* **181**, S21-S34. (doi:10.1086/668075).

293	[9] Stenberg, JA, Witzell, J & Ericson, L. 2006 Tall herb herbivory resistance reflects historic
294	exposure to leaf beetles in a boreal archipelago age-gradient. Oecologia 148, 414-425.
295	(doi:10.1007/s00442-006-0390-7).

[10] Prasad, KVSK, Song, BH, Olson-Manning, C, Anderson, JT, Lee, CR, Schranz, ME,

297 Windsor, AJ, Clauss, MJ, Manzaneda, AJ, Naqvi, I, et al. 2012 A gain-of-function polymorphism

controlling complex traits and fitness in nature. *Science* **337**, 1081-1084.

299 (doi:10.1126/science.1221636).

300 [11] Fine, PVA, Mesones, I & Coley, PD. 2004 Herbivores promote habitat specialization by

301 trees in amazonian forests. *Science* **305**, 663-665. (doi:10.1126/science.1098982).

[12] Chapin, SFI, Matson, PA & Vitousek, PM. 2011 *Principles of Terrestrial Ecosystem Ecology*. New York, Springer; 529 p.

304 [13] Belovsky, GE & Slade, JB. 2000 Insect herbivory accelerates nutrient cycling and increases

305 plant production. *Proc. Natl. Acad. Sci. U.S.A.* **97**, 14412-14417. (doi:10.1073/pnas.250483797).

306 [14] Schmitz, OJ. 2008 Herbivory from individuals to ecosystems. *Annu. Rev. Ecol. Evol. Syst.*

307 39, 133-152. (doi:10.1146/annurev.ecolsys.39.110707.173418).

308 [15] Schowalter, TD. 2011 *Insect ecology: an ecosystem approach*. 3rd ed. London, Academic
309 Press; 633 p.

310 [16] Zvereva, EL, Lanta, V & Kozlov, MV. 2010 Effects of sap-feeding insect herbivores on

growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia* 163,

312 949-960. (doi:10.1007/s00442-010-1633-1).

- 313 [17] McCall, AC & Irwin, RE. 2006 Florivory: The intersection of pollination and herbivory.
- 314 *Ecol. Lett.* **9**, 1351-1365. (doi:10.1111/j.1461-0248.2006.00975.x).
- 315 [18] Rasmann, S & Agrawal, AA. 2008 In defense of roots: a research agenda for studying plant
- resistance to belowground herbivory. *Plant Physiol.* **146**, 875-880.
- 317 [19] Zangerl, AR & Rutledge, CE. 1996 The probability of attack and patterns of constitutive and
- induced defense: A test of optimal defense theory. Am. Nat. 147, 599-608.
- 319 [20] Landsberg, J. 1989 A comparison of methods for assessing defoliation, tested on eucalypt
- 320 trees. *Aust. J. Ecol.* **14**, 423-440.
- [21] Coley, PD & Barone, JA. 1996 Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27, 305-335.
- 323 [22] Coley, PD. 1982 Rates of herbivory on different tropical trees. In *The ecology of a tropical*
- 324 forest: seasonal rhythms and long-term changes (eds. J. Leigh E.G, A.S. Rand & D.M. Windsor),
- 325 pp. 123-132. Washington, Smithsonian Press.
- [23] Brown, BJ & Ewel, JJ. 1987 Herbivory in complex and simple tropical successional
 ecosystems. *Ecology* 68, 108-116.
- 328 [24] Lamarre, GP, Baraloto, C, Fortunel, C, Dávila, N, Mesones, I, Grandez Ríos, J, Ríos, M,
- 329 Valderrama, E, Vasquez Pilco, M & Fine, PVA. 2012 Herbivory, growth strategies and habitat
- 330 specialization in tropical tree lineages: implications for Amazon beta-diversity. *Ecology* 93, S195–
- 331 S210. (doi:10.1890/11-0397.1).

[25] Lowman, MD. 1984 An assessment of techniques for measuring herbivory: is rainforest
defoliation more intense than we thought? *Biotropica* 16, 264-268.

[26] Filip, V, Dirzo, R, Maass, JM & Sarukhan, J. 1995 Within- and among-year variation in the
levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. *Biotropica* 27,
78-86.

337 [27] Dirzo, R & Boege, K. 2008 Patterns of herbivory and defense in tropical dry and rain

forests. In *Tropical forest community ecology* (eds. W.P. Carson & S.A. Schnitzer), pp. 63-78.

339 Chichester, Wiley-Blackwell.

340 [28] Shaw, DC, Ernest, KA, Rinker, HB & Lowman, MD. 2006 Stand-level herbivory in an old-

341 growth conifer forest canopy. West. N. Am. Nat. 66, 473-481. (doi:10.3398/1527-

342 0904(2006)66[473:shiaoc]2.0.co;2).

343 [29] Cahill Jr, JF, Castelli, JP & Casper, BB. 2001 The herbivory uncertainty principle: visiting

344 plants can alter herbivory. *Ecology* **82**, 307-312. (doi:10.1890/0012-

345 9658(2001)082[0307:THUPVP]2.0.CO;2).

346 [30] Hik, DS, Brown, M, Dabros, A, Weir, J & Cahill Jr, JF. 2003 Prevalence and predictability

of handling effects in field studies: results from field experiments and a meta-analysis. *Am. J. Bot.*90, 270-277. (doi:10.3732/ajb.90.2.270).

[31] Lowman, MD. 1985 Temporal and spatial variability in insect grazing of the canopies of 5
Australian rainforest tree species. *Aust. J. Ecol.* 10, 7-24.

[32] Massey, FP, Massey, K, Press, MC & Hartley, SE. 2006 Neighbourhood composition
determines growth, architecture and herbivory in tropical rain forest tree seedlings. *J. Ecol.* 94,
646-655. (doi:10.1111/j.1365-2745.2006.01127.x).

[33] Brenes-Arguedas, T, Coley, PD & Kursar, TA. 2009 Pests vs. drought as determinants of
plant distribution along a tropical rainfall gradient. *Ecology* 90, 1751-1761. (doi:10.1890/081271.1).

357 [34] Turcotte, MM, Thomsen, CJM, Broadhead, GT, Fine, PVA, Godfrey, RM, Lamarre, GPA,

358 Meyer, ST, Richards, LA & Johnson, MTJ. 2014 Percent leaf herbivory across vascular plant

359 species. *Ecology* **95**, 788. (doi:10.1890/13-1741.1).

[35] Webb, CO & Donoghue, MJ. 2005 Phylomatic: tree assembly for applied phylogenetics.
 Mol. Ecol. Notes 5, 181-183. (doi:10.1111/j.1471-8286.2004.00829.x).

362 [36] The angiosperm phylogeny group. 2009 An update of the Angiosperm Phylogeny Group

363 classification for the orders and families of flowering plants: APG III. Bot. J. Linn. Soc. 161, 105-

364 121. (doi:10.1111/j.1095-8339.2009.00996.x).

[37] Hall, TA. 1999 BioEdit: A user-friendly biological sequence alignment editor and analysis
program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* 41, 95–98.

367 [38] Stamatakis, A, Hoover, P & Rougemont, J. 2008 A rapid bootstrap algorithm for the

368 RAxML web servers. Syst. Biol. 57, 758-771. (doi:10.1080/10635150802429642).

369 [39] Stamatakis, A. 2006 RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses

with thousands of taxa and mixed models. *Bioinformatics* **22**, 2688-2690.

371 (doi:10.1093/bioinformatics/btl446).

[40] Drummond, AJ, Suchard, MA, Xie, D & Rambaut, A. 2012 Bayesian phylog	enetics with
---	--------------

- BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* **29**, 1969-1973. (doi:10.1093/molbev/mss075).
- [41] Posada, D. 2008 jModelTest: Phylogenetic model averaging. Mol. Biol. Evol. 25, 1253-
- 375 1256. (doi:10.1093/molbev/msn083).
- 376 [42] Kuhn, TS, Mooers, AØ & Thomas, GH. 2011 A simple polytomy resolver for dated
- 377 phylogenies. *Methods Ecol. Evol.* **2**, 427-436. (doi:10.1111/j.2041-210X.2011.00103.x).
- [43] Butler, MA & King, AA. 2004 Phylogenetic comparative analysis: A modeling approach for
- adaptive evolution. Am. Nat. 164, 683-695. (doi:10.1086/426002).
- 380 [44] Beaulieu, JM, Jhwueng, D-C, Boettiger, C & O'Meara, BC. 2012 Modeling stabilizing
- selection: expanding the Ornstein–Uhlenbeck model of adaptive evolution. *Evolution* 66, 2369-

382 2383. (doi:10.1111/j.1558-5646.2012.01619.x).

383 [45] Hansen, TF. 1997 Stabilizing selection and the comparative analysis of adaptation.

384 *Evolution* **51**, 1341-1351.

[46] Martins, EP & Hansen, TF. 1997 Phylogenies and the comparative method: A general

approach to incorporating phylogenetic information into the analysis of interspecific data. *Am.*

387 *Nat.* **149**, 646-667.

- 388[47] Burnham, KP & Anderson, DR. 2002 Model selection and multimodel inference: a practical
- 389 *information-theoretic approach*. 2nd ed. New York, Springer-Verlag.
- 390 [48] Revell, LJ. 2011 phytools: An R package for phylogenetic comparative biology (and other
- things). *Methods Ecol. Evol.* **3**, 217-223. (doi:10.1111/j.2041-210X.2011.00169.x).

- [49] R Core Team, 2013 R: a language and environment for statistical computing. 3.0.2. Vienna,
 Austria, R Foundation for Statistical Computing.
- [50] Wikstrom, N, Savolainen, V & Chase, MW. 2001 Evolution of the angiosperms: calibrating
- the family tree. *Proc. R. Soc. B* **268**, 2211-2220. (doi:10.1098/rspb.2001.1782).
- 396 [51] Pryer, KM, Schuettpelz, E, Wolf, PG, Schneider, H, Smith, AR & Cranfill, R. 2004
- 397 Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate
- divergences. Am. J. Bot. 91, 1582-1598. (doi:10.3732/ajb.91.10.1582).
- 399